PHYLOGENETIC STATUS OF THE IRRAWADDY DOLPHIN *ORCAELLA BREVIROSTRIS* (OWEN IN GRAY): A CLADISTIC ANALYSIS

PETER W. ARNOLD AND GEORGE E. HEINSOHN

Arnold, P.W. & Heinsohn, G.E. 1996 07 20: Phylogenetic status of the Irrawaddy Dolphin *Orcaella brevirostris* (Owen in Gray): a cladistic analysis. *Memoirs of the Queensland Museum* **39**(2): 141-204. Brisbane. ISSN 0079-8835.

Examination of *Orcaella brevirostris* from Queensland has provided new information on colour pattern, external morphometrics, skull morphology, variation in the tympanoperiotic bones and postcranial skeleton. Facial anatomy is described for the first time.

Cladistic analyses, incorporating the new information, investigated the phylogenetic position of *Orcaella*. Our results provide no support for the separation of beluga and narwhal into two different families (Kasuya,1973) nor for the proposal that *Orcaella* and *Delphinapterus* are closely related (Kasuya,1973; Pilleri et al.,1989). The position of delphinoid families in our cladograms is consistent with previous synoptic classifications (Slijper,1962, fig.36; Heyning,1989; Barnes,1990). Our results offer no support for classifications which widely separate delphinids and phocoenids (Shimura & Numachi,1987; Lint et al., 1990; Pilleri et al.,1989).

We suggest that *Orcaella* is a delphinid *sensu lato*. Comparison of characters in the two nearest outgroups (phocoenids and monodontids) suggest *Orcaella* (and other 'blunt-headed' genera) represent the most primitive Delphinidae. However, we cannot rule out the alternative that extensive convergence occurred. Extensive neoteny of the skull in *Orcaella* suggests one means by which the many apparently primitive features could occur.

☐ *Cetacea, Orcaella, periotic bone, tympanic bone, facial anatomy, neoteny, cladistics.*

Peter W. Arnold, Museum of Tropical Queensland, 70-84 Flinders Street, Townsville, Queensland 4810; George E. Heinsohn, Department of Zoology, James Cook University of North Queensland, Townsville, Queensland 4811; *received 8 November 1995.*

The phylogenetic status of the Irrawaddy dolphin *Orcaella brevirostris* (Owen in Gray,1866) remains in doubt (Marsh et al.,1989). At least eight taxonomic hypotheses are implied in various proposed classifications (Fig.1). *Orcaella* was initially classified as a porpoise in *Phocoena*. It has also been placed in a more strictly defined Delphinidae (dolphins), Delphinapteridae (with beluga *Delphinapterus leucas* (Pallas,1776)), Monodontidae (with beluga and narwhal *Monodon monoceros* Linnaeus,1758) or in the monotypic Orcellidae.

This paper addresses classification of *Orcaella*. We re-describe the skull, emphasizing neotenic characters which have confounded previous comparisons between *Orcaella* and other odontocetes. We re-examine the tympanoperiotic bones which were poorly known and describe the facial anatomy which was unknown. We assess colour patterns for possible taxonomic characters. New data on external morphometrics and the post-cranial skeleton are presented.

Incorporating this data we evaluate characters that have been used in odontocete classification. Most classifications have been based on one anatomical system (Fraser & Purves,1962; Mead, 1975; Kasuya,1973; Pilleri et al.,1989) and have produced partially conflicting classifications. Only Heyning (1989) used computerized phylogenetic analysis on a range of characters. Although he argued for a phocoenid-delphinid clade, his cladograms left relationships of the Monodontidae, Phocoenidae and Delphinidae unresolved. Gretarsdottir & Arnason (1992) also left the relationship of these 3 families unresolved. de Muizon (1988) examined extant and fossil taxa, using a comprehensive range of characters to produce 4 arrangements of the Monodontidae, Phocoenidae & Albireonidae, Kentriodontidae and Delphinidae, which were still only a subset of the possibilities. We present a cladistic analysis of the Monodontidae, Phocoenidae and Delphinidae *s. l.* Within this context we discuss affinities of *Orcaella*.

MATERIALS

Specimens of *Orcaella* were either found stranded and dead, or recovered after drowning in shark nets near Townsville. Skeletal material

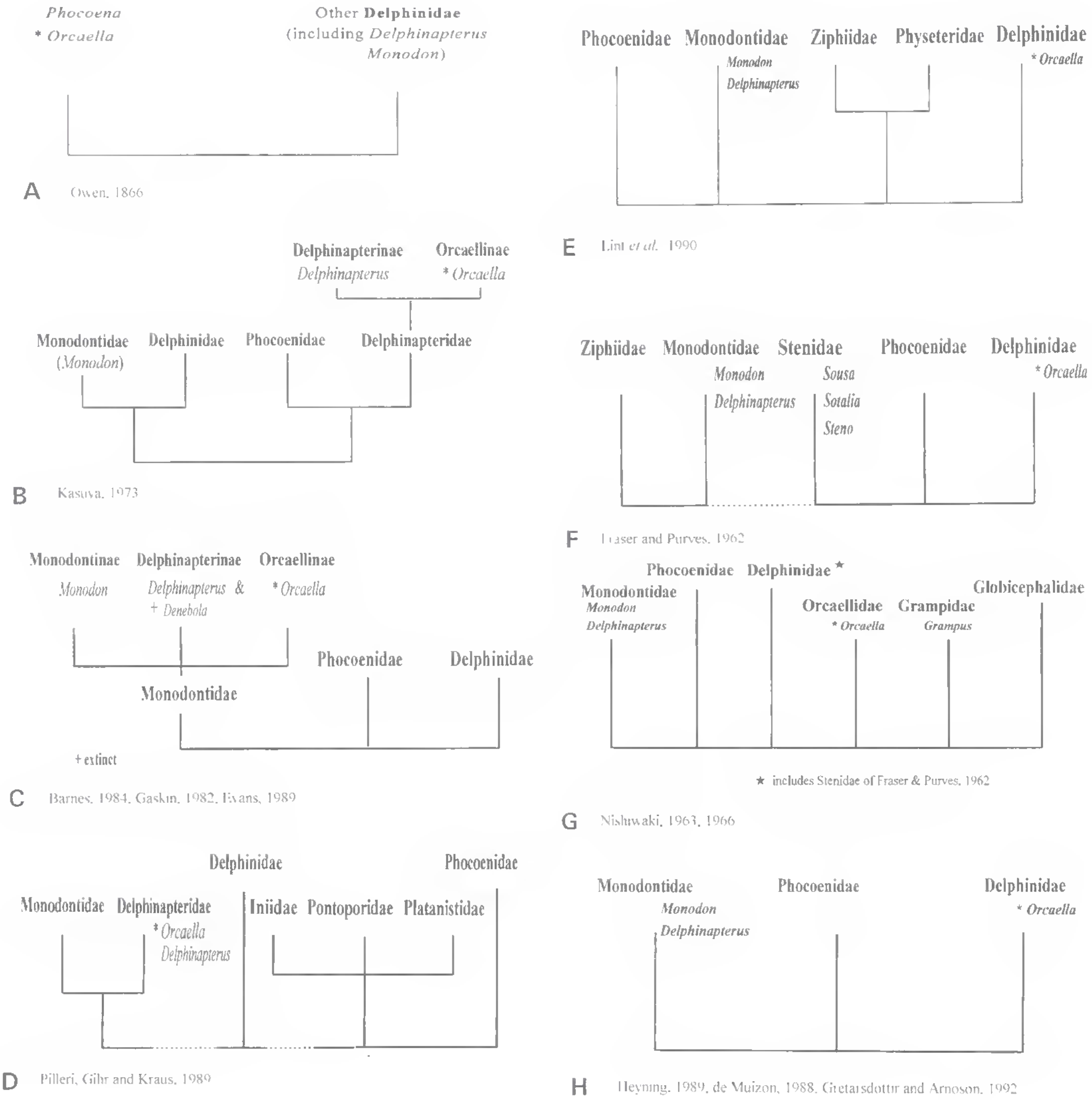

FIG. 1. Taxonomic hypotheses of phylogenetic relationship of *Orcaella* to other toothed whales. A indicates that *Orcaella* was placed within *Phocoena*, which was more broadly defined than at present. The Delphinidae was also more inclusive, containing both the beluga *Delphinapterus* and narwhal *Monodon*. The dashed lines in D separate different lineages as envisioned by Pilleri et al. (1989). The taxonomic relationships in F are derived from the table in Fraser & Purves (1962); the most generalized taxon is Ziphiidae on the left, and increasing specialization is inferred as one moves to the right. The dashed lines indicate a separation of taxa: the Physeteroidea (*Physeter, Kogia*) and Platanistoidea (*Platanista, Inia, Pontoporia, Lipotes*) were interspersed between the Monodontidae and Stenidae. The references indicated in H are only a few of the more recent ones supporting placement of *Orcaella* in the Delphinidae.

is deposited in the Queensland Museum (Paterson, 1986, 1994) (QMJ or QMJM). Most are currently held at the Museum of Tropical Queensland, Townsville; those held in Brisbane are indicated by an asterisk. Specimens collected by James Cook University staff are registered MM or CET, which numbers have been quoted in the literature; these numbers are used particularly when discussing anatomical material. If skeletal material from these specimens has been registered in the Queensland Museum, both the MM and QMJM numbers are listed below. Abbreviations for other collections are: CMN: Canadian Museum of Nature, Ottawa, Ontario, Canada; NSMNH: Nova Scotia Museum of Natural History, Halifax, N.S., Canada; UBC: Dept. Zoology, University of British Columbia, Vancouver, B.C., Canada; VA: Vancouver Aquarium, Vancouver, B.C., Canada. Measurements of beluga and narwhal are of condylobasal length and are approximate.

Orcaella brevirostris (Owen in Gray,1866) Queensland: QMJM4740; QMJM4735 (MM1004); QMJM4700 (MM006); QMJM4704 (MM012); QMJM4708 (MM021); QMJM4709 (MM025); QMJM4712 (MM030); QMJM4714 (MM032); QMJM4721 (MM 061); QMJM4725 (MM081); QMJM4726 (MM082); QMJM4727 (MM088); MM092; MM1003; QMJM11342, QMJM11343; MM1015; MM016.

Phocoenidae

Neophocaena phocaenoides (Cuvier,1829) Saudi Arabia: A. Preen,private collection.

Phocoena phocoena (Linnaeus, 1758) Nova Scotia, Canada: NSMNH973.Z.309.1; NSMNH unregistered, Oct. 26, 1982; NSMNH971.-Z.300.1; NSMNH unregistered, Crescent Beach 1977; NSMNH973.Z.310.1.

Monodontidae

Delphinapterus leucas (Pallas,1776) Quebec, Canada: Trois Pistoiles, May 11, 1983, 573 mm; DL4.85, 400 mm; DL2.86, 468 mm; Northwest Territories, Canada: CMN19556, Collinson Inlet; CMN29997, 548 mm; CMN29998-30000, Belcher I, Hudson Bay, 505, 549 and 552 mm respectively; one unregistered.

Monodon monoceros (Linnaeus,1758) Canada: CMN32278-32280, Baffin I, latter 508 mm; Arctic Biological Station MM65(at CMN); Arctic Biological Station MM66, 580 mm (at CMN); Koluktoo Bay, Baffin I: UBC 9467, 285 mm; Holman I, Northwest Territories: VA, unregistered; VA, unregistered (no data).

Delphinidae

Delphinus delphis Linnaeus, 1758 *QMJM2033, Gold Coast; *QMJM2776, Moreton Bay.

Feresa attenuata Gray, 1874 *QMJM825, Kingscliff, NSW.

Globicephala macrorhynchus Gray, 1846 *QMJM5354; CET1001, Mackay.

Globicephala melas (Traill, 1809) *QMJM4480, Point Lookout; *QMJ15.2104.

Grampus griseus (Cuvier, 1812) *QMJM9542, N. Stradbroke I; *QMJM3858, Moreton I.

Lagenodelphis hosei Fraser, 1956 *QMJM 2749, Fraser I.

Lagenorhynchus acutus (Gray, 1828) NSMNH unregistered.

Lagenorhynchus albirostris (Gray, 1846) NSMNH 72.2.343.8.

Peponocephala electra (Gray,1846) *QMJM2144, Moreton I; *QMJM6577, N. Stradbroke I; *QMJM7854; QMJM4702, Mission Beach; QMJM4730, Crystal Creek, N of Townsville.

Pseudorca crassidens (Owen,1846) *QMJM14210; *QMJM937, Townsville; MM1028.

Sousa chinensis (Osbeck, 1765) QMJM4701, Magnetic I; QMJM4703, Magnetic I; QMJM4711, Townsville; QMJM4717, Magnetic I; QMJM4728; QMJM4731, Pallarenda, Townsville; QMJM4737, Rowes Bay, Townsville.

Stenella attenuata (Gray, 1846) *QMJM6433, Moreton I.

Stenella coeruleoalba (Meyen, 1833) *QMJM3859.

Stenella longirostris (Gray, 1828) QMJM4716, QMJM4718, QMJM4719, all from off Michaelmas Cay, near Cairns.

Tursiops truncatus (Montagu, 1821) *QMJM8859; QMJM4713, juvenile, Magnetic I; QMJM4715, Magnetic I; QMJM4724, Magnetic I; MM91A, Palm I; MM1018.

METHODS

Colour pattern is described from photographs of a captive from Cairns (Dawbin,1972; Leatherwood & Reeves,1983; Mitchell,1975:911); a 1.86m ♀ (MM334) and 2.19m ♀ (MM335) from Cairns; a 2.15m ♀ (MM30), 1.87m ♀ (MM21) and 2.2 m ♀ (MM25) from near Townsville (Talbot & Steene,1984; unpubl. photographs). Based on dentinal layers in teeth, MM25 was estimated at 9 years and MM30 an estimated 8

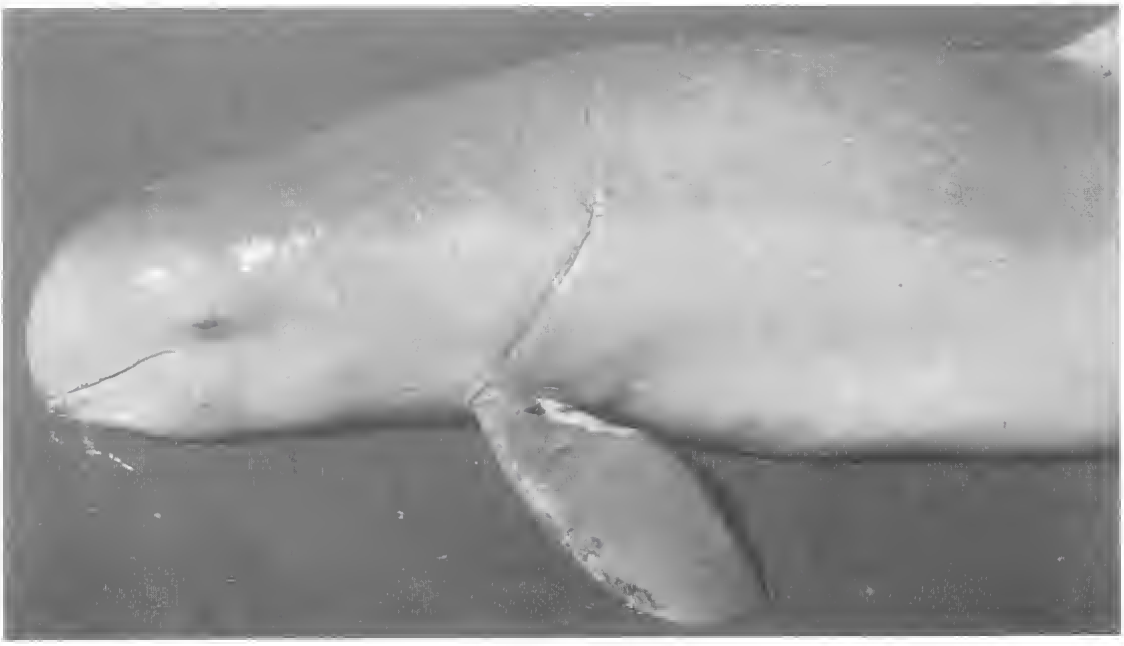

FIG. 2. Colour pattern of MM30, a 2.15 m long ♀ from Townsville.

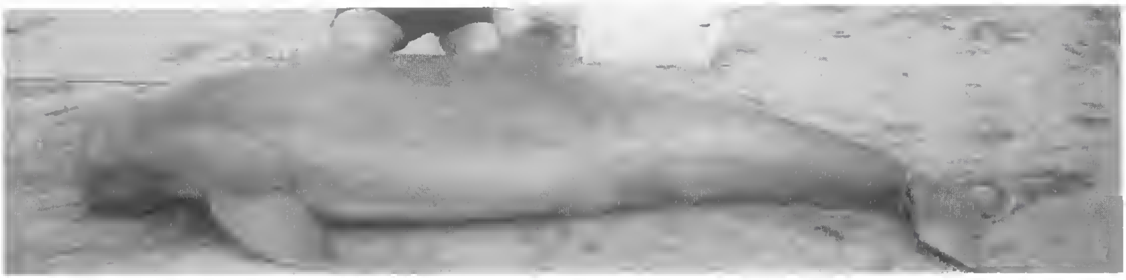

FIG. 3. Lateral colour pattern of MM25, a 2.2 m long ♀ from Townsville.

Fig 4. Ventral colour pattern of MM25, a 2.2 m long ♀ from Townsville.

years in age (Heinsohn,1979). Lengths of both animals exceeded the minimum length of confirmed sexually mature ♀♀ in the Queensland population (Marsh et al.,1989); MM335 was pregnant.

Qualitative features of the skull were compared with *Tursiops* (Rommel,1990). Standard skull measurements are as in Perrin (1975).

The angle of the posterior process of the tympanic was determined by temporarily fixing the bulla ventral side upwards on a desk. One arm of a compass was aligned along the meridional axis; the second arm was swung to lie over the lateral edge of the process. The angle so formed was traced onto paper and measured with a protractor.

The periotics were temporarily fixed dorsal side up on the stage of a compound microscope and the positions of the three cochlear apertures drawn using a camera lucida. Care was taken to orient the bulla in the same way to avoid parallex problems. The periotic triangle of Pilleri et al. (1989) was created by drawing lines between outlines of the apertures on the drawing. Angles and lengths of sides of the triangles were determined from the drawings.

Three specimens of *Orcaella* (MM333, 1.34m ♀ from Mackay, MM334, MM335, ♀♀ from Ellis Beach, Cairns) were dissected to examine the upper respiratory tract and facial region. The frozen head of MM334 was sectioned longitudinally on a band saw. The blowhole was set well to the left so the first cut was just to the left of the median line, and the second c.2cm further left. The latter section passed through the tympanoperiotic bones and pterygoid region. Facial musculature was not examined, but the relative proportions of muscle, connective tissue and 'melon' were assessed. The 'melon' was differentiated from connective tissue by its lesser vascularisation (Mead,1975) and the more fatty appearance relative to muscle and connective tissue.

Phylogenetic analyses used Hennig86, version 1.5 (Farris,1988). The implicit enumeration option was chosen to find all of the most parsimonious trees. The implicit enumeration method is time consuming for large data sets so a subset of delphinid genera were analysed. Representatives of most delphinid genera were examined; character states within the genera used to generate the cladograms cover the range of variation within the Delphinidae. Wherever possible, characters were reduced to binary values to avoid some of the problems with multistate characters. All characters were set to non-additive.

In this analysis, only extant families of odontocetes were considered as outgroups, although character states in fossil taxa have been considered in certain cases. We have not examined fossil material, and many features used have not been described in the literature available to us. To include them would result in many missing values, which can cause problems. The Kentriodontidae, which has been considered a potential sister group to delphinids, phocoenids and monodontids, cannot be clearly defined (de Muizon,1988) and may be polyphyletic. de Muizon (1993) considered the peculiar Odobenocetopsidae the sister group to the Monodontidae, but it is so highly modified that it is not relevant to our discussion.

Among extant odontocetes, the river dolphins *Platanista, Lipotes, Inia* and *Pontoporia* are considered the closest living relatives of the Monodontidae-Phocoenidae-Delphinidae (de Muizon,1988; Heyning,1989; Barnes,1990). The first two authors also demonstrated that *Platanista* is separate from the other genera; de Muizon (1990) placed it in a separate superfamily. In the present comparisons, the taxonomic status of the river dolphins can be left unresolved, but *Platanista* was considered separately from *Inia* and *Pontoporia*, and was used as the outgroup.

Character states of features used in this analysis were also determined for *Berardius*, a primitive ziphiid (Moore,1968) and *Physeter*, to determine polarity of characters. In cases where the character was not present in either physeterids or ziphiids, the character state in the fossil taxon Eurhinodelphoidea was considered to help determine the polarity. de Muizon (1990) considered the Eurhinodelphoidea as the sister taxon to Delphinida (his taxon, which encompasses all genera considered here, except *Platanista*). Reasoning in these cases is therefore not that the character is primitive because it occurs in a fossil taxon but because it occurs in a putative sister group, the members of which happen to be all extinct. Polarity decisions for all characters are justified in Appendix 2.

COLOUR PATTERN

RESULTS. A broad grey or blue-grey cape ('spinal field' of Mitchell,1970) extends from the top of the head and back downwards about half the distance to the level of the eye, continuing posteriorly to just behind the base of the dorsal fin, from which it tapers as a wedge along the upper half of the tail stock (captive animal: Daw-

FIG. 5. Dorsal view of QMJM4721, with 312.8 mm condylobasal length and 11.5 dentinal layers. Note broad transverse width of neurocranium; supernumerary bone (triangle) infilling the postnarial fossa; conspicuous triangular interparietal bone (arrow); dorsal extension of parietal bones, posterolateral to the interparietal bone; wide separation of exoccipital and frontal bones; weakly expressed telescoping (wide expanse of frontal bone exposed); prominent spina mesethmoidalis (open arrow); poorly developed nuchal crest.

FIG. 6. Dorsal view of QMJM4740. Note triangular area of spongy bone at base of rostrum, extending forward to just in front of spina mesethmoidalis; nodular nasal bones (open arrow); supernumerary bone; poor development of mesethmoid plate (posterior margin indicated by arrow) and consequent exposure of frontal bones anterior to nasal bones; wide exposure of frontal bone (triangle) between the interparietal and maxillary bones.

bin,1972; MM30: Fig. 2; Talbot & Steene, 1984:300; MM25: Fig.3). The dark grey is more extensive on the melon of MM25 than MM30 (Figs 2,3). Grey extends onto the lower jaw and throat region in the captive animal (Leatherwood & Reeves,1983:154) and MM25 (Fig.4) but in the latter, a lighter grey throat patch extends as far back as the axilla of the flippers (Fig.4). The abdominal field from the flipper region to the genital region in MM25 and MM30 (Figs 2,4) is white. The flanks between the dark cape and white abdominal field are light grey to brownish-grey (Talbot & Steene,1984; Figs 2,3); the light grey extends onto the tail stock.

MM334 has the subtle 3-tone pattern, but the dorsal fin on both sides is lighter than the back. This does not appear to be a post-mortem effect.

DISCUSSION. Underwater photographs of *O. brevirostris* from the Mahakan River, Indonesia (Tas'an & Leatherwood,1984; unpubl. photos by Dr. A. Preen) do not show the three tone colour. This may be a real difference, or simply reflect the difficulty in differentiating subtle shading with the rapid loss of contrast underwater.

Anderson (1879, pls 25, 25a) described *O. brevirostris* as 'dark slaty-blue, nearly black, and very little paler on the ventral surface'. It is unclear how long his specimens had been dead; postmortem darkening of cetaceans can be substantial (Pilleri,1976). Anderson (1879) noted that living *O. fluminalis* (=*brevirostris*) were more lightly coloured . The dark grey to black colouration of *Orcaella* needs to be confirmed on living animals.

The subtle 3-tone colouration of Queensland *Orcaella* may be found in juveniles of several dolphin genera, becoming fainter or lost in adults. However, given the sizes and ages of the animals examined, the colour patterns we describe appear to be characteristic of adult animals.

Mitchell (1970) considered the three-tone pattern as the 'common baseline from which to interpret most of the patterns found within the Delphinidae'. Its occurrence in *Orcaella* thus can not be used as evidence for relationship to other delphinid genera. The extension of grey onto the lower jaw and throat in *Orcaella* is similar to the pattern in *Globicephala, Pseudorca, Peponocephala* and *Grampus*. None of the *Orcaella* had a throat chevron, midventral stripe or genital patch as occurs in those genera (Minasian et al., 1987; Mitchell 1970), although MM25 had a vague light grey throat patch similar to a throat chevron. The throat chevron is not restricted to the 'blunt- headed' whales; *Tursiops truncatus* cf *aduncus* may have a distinct throat chevron (G.J.B. Ross pers. comm.). The photographs of *Orcaella* are not of sufficient quality to show unequivocally more specialised features such as spinal blaze, bridles or flipper stripe. In this case, colour pattern is of little taxonomic use.

SKULL

RESULTS

REDESCRIPTION OF SKULL. Values presented below are based on 14 animals from central Queensland, Australia with condylobasal lengths from 297.7–334.8mm and an estimated age (based on dentinal layers) of 3–28 years. An additional skull of a newborn, 232.1mm condylobasal length, was examined for non-mensural characters, but measurements of this specimen were excluded from the descriptive statistics.

Unless otherwise indicated, values are percentages of condylobasal length, based on measurements on the left side of the skull. *Orcaella* has cranial asymmetry as is general in delphinids; this will be considered in detail in a separate publication.

DORSAL ASPECT. The neurocranium is broad (Fig.5), 65.6% (62.6–68.0%) at the postorbital process of the frontal which is usually the widest point of the skull. Zygomatic width is 65.4% (63.2–68.3%).The lacrymal bones extend forward from the maxillary bones to form the lateral border of prominent antorbital notches, 4.0% (2.8–4.5%) deep.

The rostrum is 44.4% (43.2-45.5%)long and 37.6% (34.4–39.8%) wide at the base. Premaxillaries as a percentage of rostrum width are 50.5% (47.0–57.6%) at the base, 62.8% (60.0–65.9%) at 0.25 length, 61.2% (58.1–65.1%) at 0.5 length and 65.0% (56.0–73.1%) at 0.75 length. The spongy, triangular area of the rostrum, bounded laterally by 2 oblique ridges, extends just beyond the proximal quarter of the rostrum (Fig.6).

The premaxillaries continue onto the cranial vault, showing distinct asymmetry at the point of maximum width: the left premaxillary is 4.3% (2.4–5.7%) wide and the right 8.5% (7.6–9.1)% wide at this point. There is a prominent exposure of the frontals between and behind the ascending processes of the maxillaries (Fig. 5).

The vertex is composed mainly of the frontals, with a median suture deflected to the left (Fig.5). It forms an ill-defined ridge running along the body axis between the ascending processes of the maxillaries. The nasal bones are peculiar nodules, often two on each side of the vertex (Fig.6), from 7.3–15.6mm long by 6.4–14.0mm wide. The nasal bones sometimes coalesce, but always retain their nodular appearance (Fig. 7). The postero-medial pair of nasal nodules are at the apex of the vertex while the anterolateral nasal nodules are on the anterior face of the vertex. The anterior face of vertex has a shallow postnarial pit, usually filled in by a supernumerary bone 6.0-22.0mm long by 5.4–17.8mm wide (Figs 5–7).

The mesethmoid plate is generally poorly developed (Figs 5–8), leaving much of the anterior face of the vertex exposed (Figs 6,8). An elongate, shallow fossa occurs laterally in this space, between the apical nasals and the mesethmoid plate (Fig.8). When the mesethmoid plate is more extensive, the fossa excavates its posterolateral margin, leaving a median extension of the plate which reaches back to the supernumery bone on the vertex (Fig.7).

The frontals are always distinctly separated

FIG. 7. Oblique anterodorsal view of vertex, QM JM4714. Note nodular, partially coalesced nasal bones (open arrow); development of mesethmoid plate (posterior margin indicated by triangle); and maxillary intrusions (arrow) along anterior margin of superior nares.

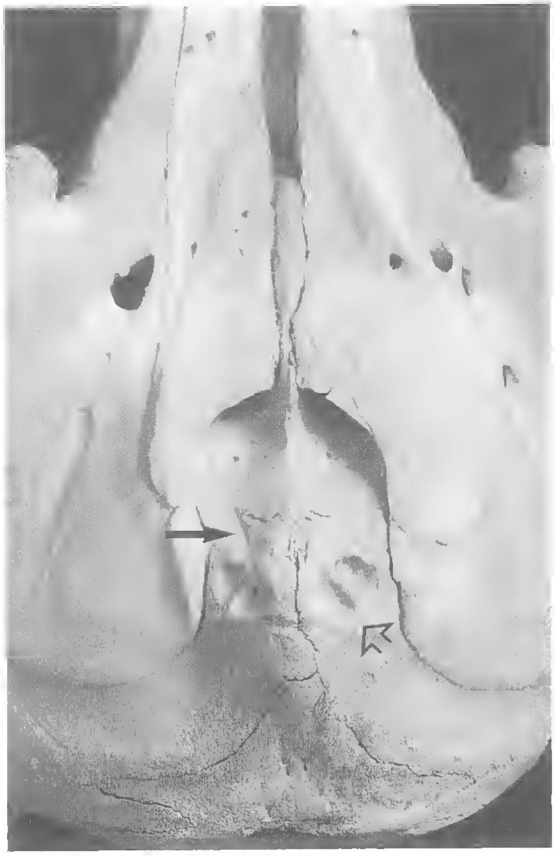

FIG. 8. Dorsal view of QMJM4735. Note poor development of mesethmoid plate (posterior margin indicated by arrow); shallow lateral fossa between mesethmoid plate and depressions for the nasal bones (open arrow); prominent interparictal bone.

from the supraoccipital by prominent dorsal extensions of the parietal bone and a triangular interparietal bone (Figs 5,8).

Anteromedial borders of the superior nares are edged by maxillary intrusions 8.2% (5.8–10.0%) long and 2.4% (1.3-3.5%) wide (Figs 5–8). These intrusions are weakly size dependent (r=0.649 for left maxillary intrusion length vs condylobasal length). A very prominent spina mesethmoidalis extends anterior to the bases of the antorbital notches and widely separates the premaxillaries (Figs 5,6,8). Braincase width is 49.8% (47.0–54.0%) across the parietals and 51.3% (48.2–55.2%) across the squamosals.

LATERAL ASPECT. The skull is deep, 57.2% (55.3–60.6%) from vertex to the left paroccipital crest.

The orbit is prominent (Fig. 9), 15.8% (15.0–17.1%) between the preorbital and postorbital processes of the frontal bone. The jugal is stout, fitting within a prominent notch on the anterior face of the zygomatic arch. The maxillary bone over the lacrymal and preorbital process of frontal is raised to a variable extent; when it is extensively developed it imparts a concave profile to the supraorbital plate of the maxillary bone.

The temporal fossa is bounded dorsally and posteriorly by a weakly developed temporal crest. The majority of the fossa is bounded medially by parietal and base of the squamosal (Fig.9). The zygomatic arch of the squamosal is prominent, with an extensive mastoid section laterally and a wide post-glenoid space (Fig.9). The paroccipital

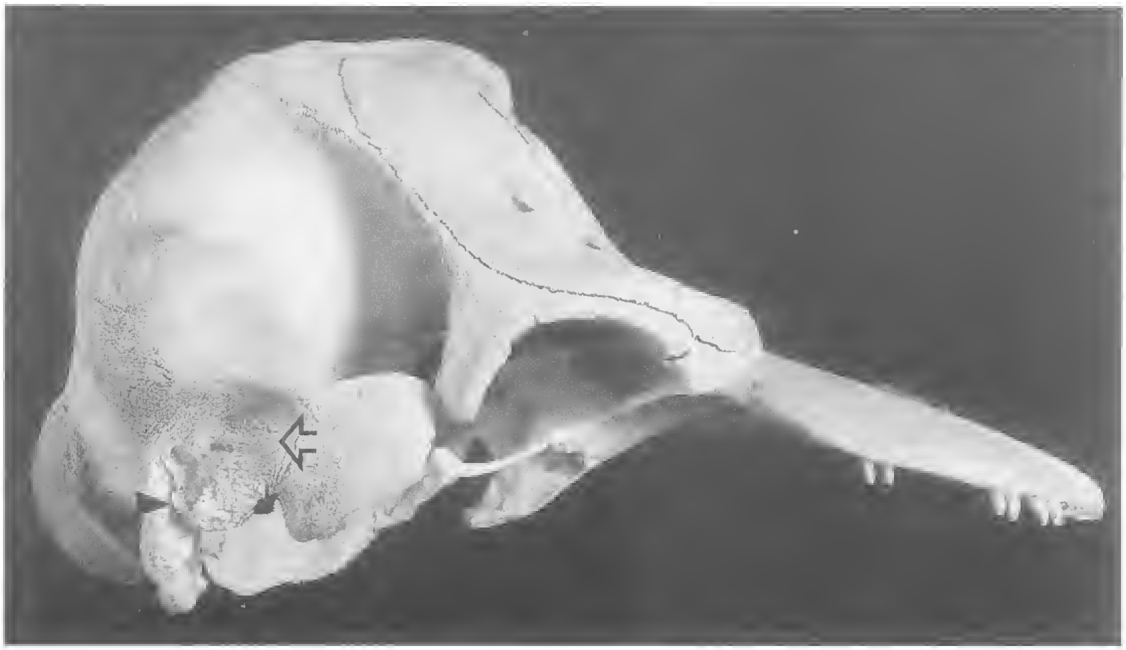

FIG. 9. Lateral view of QMJM4721. Note prominent orbit; robust jugal bone (broken); oblique orientation of occipital condyles; poorly developed temporal crests; ventral orientation of paroccipital process of exoccipital; fissure (triangle) between exoccipital and prominent mastoid portion of zygomatic arch (open arrow).

process of the exoccipital is directed outwards and ventrally, with minimal intrusion anteriorly onto the zygomatic arch. A deep, usually Y-shaped fissure separates the mastoid portion of the squamosal from the paroccipital process of the exoccipital (Fig. 9). The occipital condyles are prominent and directed ventrally at c.45° to the skull axis (Fig.9). Braincase length is 43.1% (42.0–44.9%).

VENTRAL ASPECT. The posterior of the palate contains triangular lateral lobes of the palatine bones, each with a prominent foramen (Fig.10) which forms the anterior end of a channel extendeding dorsally and backwards to the pterygopalatine fossa.

The lateral lobe of the palatines extends posterolaterally as a wing-like process (Figs 10,11) 11.0.% (9.3–12.5%) long along its anterior margin, and underlying an extensive preorbital cavity formed between the maxillaries and presphenoid/frontal bones (Fig.11). This cavity extends dorsally as a lobe, more extensively developed on the right than the left side.

The pterygoid hamuli are distinctly separated by triangular medial lobes of the palatine bones (Figs 10,11). The palatines flank the vomer and spina mesethmoidalis, which is often incompletely covered by the vomer. Sometimes the vomer is visible between the sutures of the palatines and maxillary bones (Fig.12) but in most cases it is indicated only by a pit.

A medial flange extends from the pterygoid hamuli (Figs 10-12), bringing them to within 1.0% (0.6–1.5%) of one another and almost completely covering the inferior nares.

The lacrymal bones are massive (Figs 10,12), 12.4% (10.2–15.0%) long by 14.4% (13.4–15.1%) wide. The frontal bones form a prominent obliquely transverse ridge (Fig. 11) without an optic groove or channel. The optic foramen is incompletely separated from the anterior lacerate foramen by a short vertical bony bridge formed by the fused presphenoid-orbitosphenoid bones. The alisphenoid bone is a prominent plate (Fig. 12), forming the anterior margin of the foramen ovale (posterior margin of foramen provided by an extension of the basioccipital).

The zygomatic arch has an extensive tympanosquamosal recess (Fig. 12). The falciform process is reduced, 3.9% (3.0-5.1%, n=10) long by 3.7% (2.8–4.9%, n=7) wide. It runs parallel to the alisphenoid, rather than ventrally and is not closely associated with the periotic bone. The postglenoid space contains a wide groove for the auditory meatus and a prominent triangular mas-

FIG. 10. Ventral view of QMJM4708. Note triangular anterior portion of lateral lobe of palatine, containing palatine foramen (arrow); posterior wing-like extension of lateral lobe of palatine (triangle); complete separation of medial and lateral lobes of palatines by pterygoid (open arrow); separation of pterygoid hamuli by medial lobes of the palatines; medial flanges on pterygoid hamuli.

FIG. 11. Ventral view of QMJM4721. Note wing-like posterior extension of lateral lobe of palatine; medial flange of pterygoid hamuli (triangle);transverse frontal ridge anterior to optic channel; large pre-orbital space for dorsal extension of pre-orbital lobe (curved arrow); mastoid pad of zygomatic arch (broad arrow); prominent groove for external auditory meatus (thin arrow); deep pit medial to mastoid pad (open arrow).

toid pad (Figs 11,12), the latter providing articulation for the tympanoperiotic bones. Between the base of the squamosal, just medial to the mastoid, and a ventral extension of the parietal is a deep pit (Figs 11,12). In QM JM4709, this is one end of a channel which opens on the back of the skull in the suture between the squamosal and parietal bones. The cranial hiatus is wide in young animals, but could be completely infilled in older animals.

MANDIBLE (Fig. 13). Mandibles are 76.7% (75.4–78.6%) long, with coronoid depth 23.6% (22.3–25.1%). The mandibular fossa is 32.8% (29.9–35.4%)long, while the mandibular symphysis is 7.7% (5.6–11.4%) long by 8.3% (6.5–9.0%) deep.

Alveolar/tooth counts (mean, rounded to whole number, followed by range in parentheses) are

18 (17–20)/ 18 (16-20) n=14
17 (15–19)/ 17 (16-18) n=13.

Total alveolar/tooth counts are 66–78. Apparently the central teeth erupt first; in MM334 the erupted tooth count is only 15/13 11/14.

COMPARISON WITH TYPE SPECIMEN. Owen's (1866) description of the vertex and the accuracy of his pl.9, fig.2 are confirmed by the holotype (R. Sabin pers comm.; Fig.14). The most significant differences in the vertex, as compared with Australian material, are the 2 elongate antero-posteriorly compressed nasal bones (cf multiple nodular nasal bones) and well-developed mesethmoid plate, abutting on the nasal bones (cf reduced mesethmoid plate).

FIG. 12. Ventral view of QMJM11342. Note vomer insunk between medial lobes of palatine (arrow); incomplete separation of medial and lateral lobes of the palatines; wing-like posterior extension of palatine; medial flange on pterygoid hamuli; prominent alisphenoid; extensive tympano-squamosal recess of zygomatic arch (triangle); mastoid pad and groove for external auditory meatus.

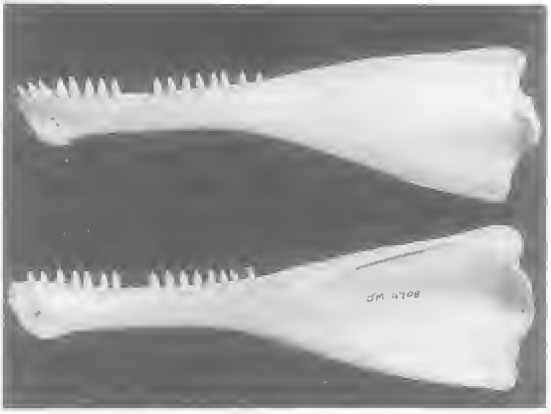

FIG. 13. Lateral and medial views of mandible of QMJM4708.

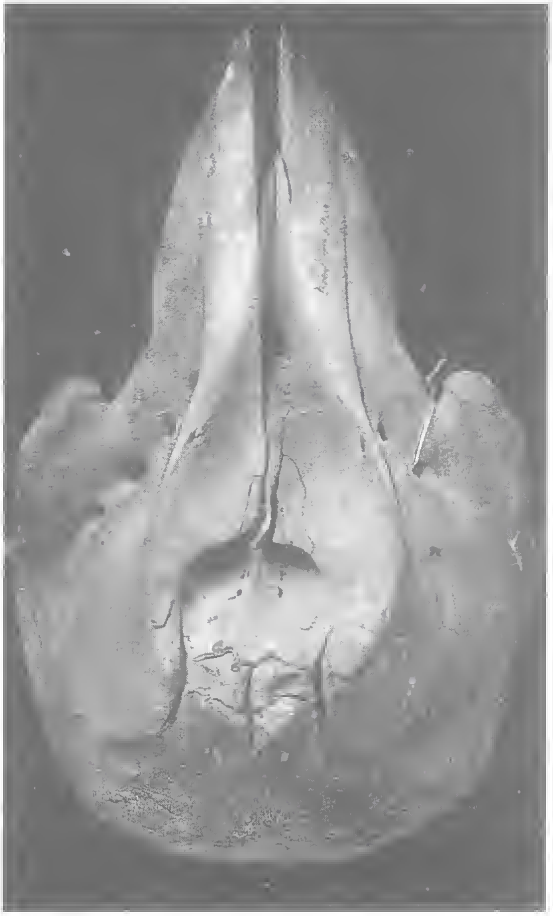

FIG. 14. Dorsal view of BM(NH)1865.4.20.1, holotype of *Orcaella brevirostris*.

DISCUSSION

NEOTENIC FEATURES OF THE SKULL. Winge (1921) noted that *Orcaella* 'gives the impression of being a dwarf form with noticeably large braincase in proportion to the face'. This appearance is due to massive development of the skull roof. Comparison of newborn and mature *Orcaella* (Fig. 15) with newborn and adult *Peponocephala* (Fig.15) and *Feresa* (Fig.15) show this to be a retained juvenile feature. In all these cases, the interparietals and parietals form major components of the skull roof and much of the frontal bone is exposed in the newborn animal. In adult *Peponocephala* and *Feresa*, the parietals have been excluded from the roof of the skull and the interparietal is reduced or completely obscured by other bones; telescoping of the maxillaries has advanced to cover much of the

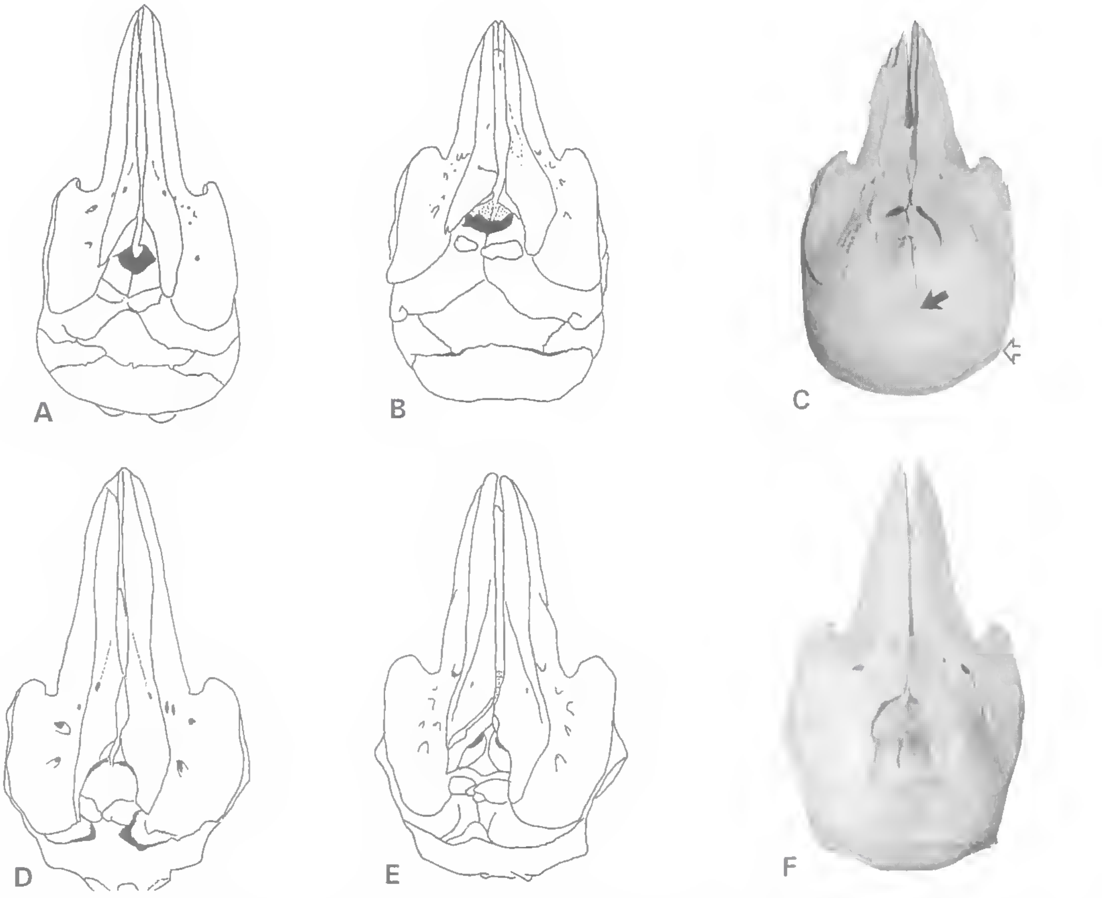

FIG. 15. Neoteny in *Orcaella*. Note similarity in development of interparietal (arrow), dorsal extension of parietal (open arrow), extensive exposure of frontals (weak telescoping of maxillary and premaxillary bones) in the newborn *Peponocephala, Feresa* and *Orcaella* (A,B,C). In adult *Peponocephala* and *Feresa* (D,E) the dorsal exposure of the interparietal is reduced or obliterated; the dorsal extensions of the parietals are similarly overridden; the frontals become covered by the maxillaries and premaxillaries. In contrast, adult *Orcaella* (F) retains juvenile features in the form of extensive dorsal exposure of the interparietal & dorsal extensions of parietals, weak telescoping of skull. *Peponocephala* redrawn from Dawbin et al. (1970), *Feresa* from Perrin & Hubbs (1969). Juvenile *Orcaella* is QMJM11343, a disarticulated skull which was re-assembled; positions of the bones could be determined by their impressions on the braincase.

frontal bone. Similar change with growth is evident in *Pseudorca* (Cowley,1944, pl.1), *Globicephala melas* (Fraser,1950, pl.2), *Monodon* (Eales,1950, fig. 15; van Beneden & Gervais, 1868–1879, pl.45, fig.1) and *Phocoena phocoena* (van Beneden & Gervais,1868-1879, pl.43, fig.5). In adult *Orcaella*, however, dorsal exposure of the interparietal and parietals is maintained, and there is only weak telescoping (Figs 5,14,15; Marsh et al.,1989, fig.3) of the skull, much as in the newborn or juvenile.

This discrepancy between *Orcaella* and other genera can further be demonstrated by comparing proportions of interparietal length and width in *Orcaella* and *Pseudorca* of known age. *Orcaella* maintains the proportional length and width of the interparietal in the oldest animals examined (Fig.16). *Pseudorca*, while having a greater dorsal exposure of the interparietal than most odontocetes, shows a significant decrease in interparietal length after two growth laminae and width after 8-14 dentinal laminae (Purves & Pilleri, 1978, fig.16).

Nuchal and temporal crests are poorly defined in *Orcaella*, which is general in juvenile skulls (as in newborn and adult *Pseudorca* (Cowley,1944, pl.1), *Peponocephala* (Dawbin et al.,1970, fig.7) or *Feresa* (Perrin & Hubbs,1969, fig.4)). Barnes (1985) noted these features as paedomorphic in phocoenids.

Also evident from the growth series of odontocetes is the progressive development of the mesethmoid plate on the front of the braincase. In adult *Orcaella*, the mesethmoid can completely cover the anterior face of the braincase (Fig.14). In Queensland material much of this area is left exposed. The mesethmoid plate is poorly developed in a specimen of *Orcaella* from Melville Bay, Northern Territory (Johnson, 1964, pl.14). Two specimens in the Western Australian Museum also have a poorly developed mesethmoid plate (J.L. Bannister, pers. comm.). This suggests that poor development of the mesethmoid is another retained juvenile feature which may be best expressed in Australian animals. If it were a truly primitive character, one would not expect to see any examples in which the mesethmoid completely covered the front of the braincase.

Telescoping of the skull (Miller,1923) is weak in newborn odontocetes, with the ascending processes of the maxillaries still far forward, leaving a large amount of the frontals exposed. In most genera, telescoping is increasingly expressed in older animals, but in *Orcaella* telescoping resembles that of juvenile odontocetes, with the frontals widely exposed.

The short rostrum of *Orcaella* may be a retained juvenile feature. According to Tomilin (1967), the mean rostrum length as a proportion of condylobasal length for adults and 'young' of *Grampus* were 0.501, 0.457; *Globicephala* 0.507, 0.474; *Pseudorca* 0.481, 0.475; and *Orcinus* 0.500 (adult ♂), 0.471. The mean value for proportion of rostrum length in *Orcaella* (0.444) is thus closer to the values for juveniles of other blunt-headed dolphins (although similar to values for adults of some phocoenids).

Most features listed as neotenic relate to the roof of the braincase. DeBeers (1937 in Pilleri et al., 1982) contrasted the dermal bones of the skull roof and the substitution bones, preformed in cartilage, at the base of the skull. He further noted that it was the dermal bones in which differentiation and growth reflected the growth of the brain, wwhile the bones at the skull base were independent of brain growth. Thus neotenic features should be most obvious in the dorsal aspect of the skull, as documented here for *Orcaella*.

Lloze (1982) documented the os wurmiens ('small supernumerary bones...situated between various bones of the cranium') in *Orcaella*; they also occur on some Queensland specimens. Lloze suggested that they may be space 'fillers', associated with the growth of the braincase. The braincase is proportionately larger in *Orcaella* than in most odontocetes (Lloze, 1982). An enlarged braincase is generally recognised as a neotenic feature (Gould, 1977) and we suggest it is a retained juvenile feature in *Orcaella*.

Oeschlager (1986) noted a proportional decrease in the mastoid portion of the squamosal with age in *Tursiops* and *Lagenorhynchus*, which suggests that the large postglenoid space in *Orcaella* is a neotenic feature. We think this is unlikely for two reasons. First, a proportional decrease in the mastoid was not obvious in a small series of *Tursiops* skulls available to us. Moreover, the posteroventral orientation of the paroccipital process of the exoccipital in *Orcaella* and the large basicranial space, as well as the extent of the postglenoid space, exceeds that in newborn odontocetes of other delphinoid genera which we have examined, with the exception of *Neophocaena*.

Deflexion of the occipital condyles (Fig.9), otherwise known only in *Neophocaena*, may reflect the enlargement of the braincase, but it probably is not a retained juvenile feature as there is no indication from growth series of *Orcaella* or other genera that the condyles move from a ventral to posterior position.

IMPLICATIONS OF NEOTENY. *Orcaella*'s skull is characterised by large braincase and short rostrum as in Gray's (1866) diagnosis. If these are retained juvenile features as we suggest, then it may not be valid to make comparisons of *Orcaella* with adults of other genera for taxonomic purposes. It is not surprising that published attempts have been equivocal since juvenile skulls of odontocete genera are more similar than are skulls of adults.

de Muizon (1988) placed *Orcaella* in the Globicephaliinae, on dilation of the premaxillae at the tip of the rostrum. However, the premaxillary width of *Orcaella* at 0.75 rostrum length is comparable to that in delphinids (pers. obs.) and is closer to that of juvenile *Globicephala*.

de Muizon (1988) and Barnes (1990) considered a well-developed mesethmoid plate to be diagnostic features of delphinids. Although the *Orcaella* mesethmoid plate can completely fill the posterior border of the nares (Fig.14), it is usually poorly developed in Australian specimens, leaving much of the anterior slope of the vertex exposed. de Muizon (1988) and Barnes (1990) suggested that the greater development of

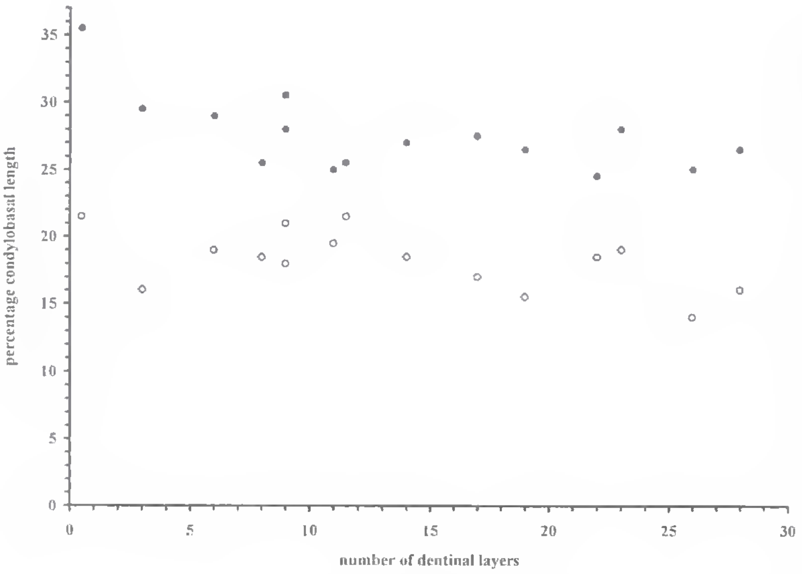

FIG. 16. Variation in width (closed circles) and length (open circles) of interparietal in *Orcaella* as percentage of condylobasal length, compared with age as expressed by dentinal layers in teeth. The newborn animal QMJM11343 was not aged, and is arbitrarily placed at 0.5 years. Note the minimal reduction in both width and length of the interparietal.

the mesethmoid plate pushed the nasals to an apical position on the vertex and resulted in transverse compression of the nasal bones. Despite the weaker development of the mesethmoid plate in our material, the posterior pair of nasal bones of *Orcaella* are apical, so position of the nasals may not be linked to development of the mesethmoid. The nasals are, however, reduced in size, nodular, and not compressed. They differ from the type of *O. brevirostris* (Fig. 14) and from *O. fluminalis* (Anderson, 1879, pl. 42, fig.2). van Beneden & Gervais (1868–1879, pl. 64, fig.2a) illustrated 2 reduced nodular nasals in *Orcaella* from the Mekong River; Lloze (unpubl. MS) also noted that 'the rudimentary nasal bones are formed by two little bones which fuse with advancing age'. Thus reduction of the nasals may be a generic feature, although it seems particularly well shown by Queensland specimens. Reduction of the nasals seems to occur in some *Cephalorhynchus hectori* (van Beneden, 1881) (pers. obs.) and Perrin (pers. comm.) noted a *Stenella frontalis* (Cuvier, 1829) with two nasals on the right. Perhaps the nodules represent multiple sites of ossification (G.J.B. Ross pers. comm.) which may remain discrete. If so, this could be another neotenic feature.

The postnarial fossa, infilled by a supernumary bone, and shallow lateral fossae on the anterior slope of the vertex have not been described in *Orcaella*, although the former was illustrated by Johnson (1964, pl. 14). This may be because of the greater development of the mesethmoid in animals examined to date from southeast Asia. Postnarial fossae have been described in Kentriodontidae, but these appear to be different from the present case, based on de Muizon (1988, fig.21). The lateral fossae are similar to fossae of phocoenids, *Delphinapterus* and *Monodon* (de Muizon, 1988, fig.25). These fossae in *Orcaella* do not, however, provide evidence for its close relationship to phocoenids or monodontids. Rather, they probably reflect the weak mesethmoid plate in our material, leaving much of the vertex exposed. In a juvenile *Tursiops* (QMJM4713), with the mesethmoid still weakly developed, there are similar shallow imprints or fossae between the mesethmoid plate and nasals.

BASICRANIAL CHARACTERS. Since the basal skull bones are less subject to modification by brain growth, perhaps they offer better characters for assessing relationships of *Orcaella*. Unfortunately, positions of the sphenoidal bones are rarely evident from photographs and we have been able to examine only a limited series of specimens, usually without juveniles.

In ventral view (Figs 10–12), enclosure of the palatine foramen within the triangular lateral lobes of the palatine is characteristic. This appears to be the minor palatine foramen of Evans & Christensen (1979). In sagittal section (Fig.33) the palatine contains a highly vascularised excavation. In *Tursiops* (Rommel, 1990) and in specimens of *Sousa*, *Globicephala*, *Pseudorca*, *Stenella*, *Delphinus*, *Peponocephala*, *Grampus*, and *Feresa* the minor palatine foramen is not visible and there is only the major palatine

TABLE 1. Summary statistics of measurements, based on 21 tympanoperiotic bones from 11 animals. Numbering of characters corresponds to sequence in Appendix 1, which contains full data and details of measurements.

CHARACTER	MEAN	RANGE
(1)Standard length tympanic bone	34.82	33.05-36.50
(2)Tip to posterior end of inner posterior prominence	95.42	93.15–99.71
(3)Distance from posteroventral tip of outer posterior prominence to tip of sigmoid process	62.01	58.07–66.26
(4)Distance from posteroventral tip of outer posterior prominence to conical process	43.95	39.77–47.41
(5)Width bulla at level of sigmoid process	57.80	53.94-60.98
(7)Width across inner and outer posterior prominences	58.81	53.94-62.61
(8)Depth interprominential notch	30.26	22.52-36.19
(10)Width posterior branch of lower tympanic aperture	6.54	5.28-8.89
(13)Standard length periotic bone	35.69	31.00-38.20
(14) Thickness superior process at level of upper tympanic aperture (excluding spongy bone shelf over aequeductus vestibuli)	35.55	31.97-41.38
(15)Width across cochlear portion and superior process at level of tympanic aperture	55.13	49.30-64.09
(19)Length of cochlear portion of periotic	42.65	38.95-46.62
(22)Standard length as percentage of standard length of tympanic bone	102.62	92.00-112.02
(23)separation of foramen singulare and aequeductus Fallopii (n=12)	14.10	9.08-19.01
(25)Anteroposterior length of fundus of the internal auditory meatus	28.75	22.04-38.33
(26)Width of foramen ovale (n=9)	5.55	3.74-7.00
(27) Width of foramen rotundum	8.85	7.54-10.29
(28) Width of head malleus (n=9)	10.86	8.53-12.02

foramen on the suture of the palatine lobe with the maxillaries. However, both foramina may be present in delphinids (Perrin pers. comm.) and their development may be a variable feature.

The lateral and medial lobes of the palatines are widely separated and the maxillary can directly contact the pterygoid hamuli, totally separating the medial and lateral lobes of the palatines (Fig.10). de Muizon (in press) notes that separation of medial and lateral lobes of the palatines is unusual among odontoectes. The separation of the pterygoids in *Orcaella* is by the medial lobes of the palatines, which surround and may override the vomer so that it is no longer visible from below (but see Fig. 12). This resembles the construction in delphinids such as *Sousa*, *Tursiops* and *Stenella*, and is distinct from other odontocetes with widely separated pterygoids (Pilleri et al., 1982). In phocoenids and *Delphinapterus*, the pterygoid hamuli are relatively small and do not deeply excavate the palatine, so the connection between median and lateral lobes is broad. In the long-snouted dolphins, although the pterygoids deeply excavate the palatines the latter are displaced forward onto the rostrum so that medial and lateral lobes of the palatine remain connected. Partial to complete separation of the lobes can occur in *Grampus* (Tomilin, 1967) and *Feresa* (QMJM825). Perrin (pers. comm.) noted complete separation of the medial and lateral lobes in a juvenile *Globicephala macrorhynchus*; the lobes are also separate in a Southern Hemisphere *G. melas* (QMJ15.2104). This separation may result from deep excavation of the pterygoids abutting onto a shortened rostrum of the skull, but it is not a simple relationship. *Monodon* (Tomilin, 1967; pers. obs.) and the delphinid *Pseudorca* (adult and newborn: Cowley, 1944) have well developed pterygoid hamuli and a short rostrum but the median and lateral lobes of the palatines remain broadly connected.

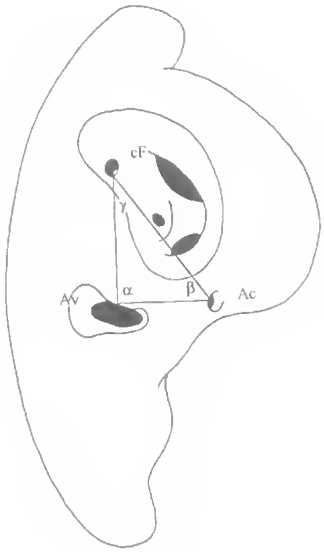

FIG. 17. Diagram of periotic of *Orcaella* in dorsal view showing features of the periotic triangle. Abbreviations: cF=canal for facial nerve (=aquaeductus Fallopi); Av=aquaeductus vestibuli (=ductus endolymphaticus); Ac=aquaeductus cochleae; alpha, beta and gamma indicate angles as defined by Pilleri et al., 1989.

TABLE 2. Angles of the periotic triangle, measured from camera lucida drawings. Abbreviations: PA, AW: different observers; L=left; R=right; #1, #2: measurements by same observer.

SPECIMEN NUMBER		α	β	γ	γ/β
QMJM4706	L(PA)	91	55.5	33.5	60.4
QMJM4706	(AW)	88	62	30	48.5
QMJM4706	R(AW)	82	63	35	55.6
QMJM4700	L(AW)	80	70	30	42.9
QMJM4700	R(AW)	78	67	35	52.2
QMJM4712	L(PA)#1	89	59	31	52.5
QMJM4712	(PA)#2	84	55.5	40.5	73.0
QMJM4705	L(AW)	86	60	34	56.7
QMJM4705	R(AW)	90	59	31	52.5
QMJM11343	L(AW)	77	66	37	56.1
QMJM11343	R(AW)	77	66	31	56.1
QMJM4704	R(PA)	90	47	43	91.5
QMJM4708	R(AW)	72	54	54	100.0
QMJM4709	L(AW)	78	63	39	61.9
QMJM4709	R(AW)	102	48	30	62.5
QMJM4740	L(PA)	93.5	47	39.5	84.0
QMJM4721	L(PA)	93.5	48.5	38	78.4

TABLE 3. Lengths of sides of the periotic triangle, measured from camera lucida drawings.

SPECIMEN NUMBER		Av-cF	Av-Ac	%Av-Ac/Av-cF
QMJM4709	(AW)	59	40	67.8
QMJM4709		50	36	72.0
QMJM4708	(AW)	39	39	100.0
QMJM4704	(PA)	48	44	91.7
QMJM11343	(AW)	60	40	66.7
QMJM11343		54	37	68.5
QMJM4705	(AW)	61	39	63.9
QMJM4705		55	35	63.6
QMJM4706	(PA)	50	35	70.0
QMJM4706	(AW)	55	32	58.2
QMJM4712	(PA)	48	38	79.2
QMJM4700	(AW)	58	38	65.5
QMJM4700		57	31	54.4
QMJM4740	(PA)	52	45	86.5
QMJM4721	(PA)	49	40	81.6

The posterior wing of the lateral palatine of *Orcaella* is unusual in its separation from the rest of the braincase. A posterior extension of the palatine is found in *Globicephala*, *Feresa*, and *Pseudorca* (Purves & Pilleri, 1978, fig. 18) where it forms a bridge under the optic canal. However, in those genera, the palatine wing is oriented vertically (in adults examined), whereas in *Orcaella* it is parallel with the bones of the basicranium, as a free wing-like structure, which appears to be flattened against the bones of the skull. The basicranium also appears to be flattened. The relatively long paroccipital crest, almost at right angles to the main axis of the skull, creates a very large basicranial space, which may cause a more lateral (flattened) orientation of the bones of the skull base. For instance, the falciform process of *Orcaella* is flattened against the braincase. This differs from the delphinids examined (*Tursiops, Sousa, Globicephala, Pseudorca, Stenella, Delphinus, Peponocephala, Grampus*, and *Feresa*) which all have a strong ventral deflexion of the falciform process, curving around the anterior of the periotic bone.

An extensive cavity between the maxillaries and frontal/presphenoid can accommodate a dorsal extension of the preorbital lobe. This feature resembles the extension in phocoenids (Fraser & Purves, 1962). However, there is a similar expansion of the lobe in delphinids such as *Pseudorca* (pers. obs.) and juvenile *Globicephala macrorhynchus* (Perrin pers. comm.).

The pterygoid hamuli have medial flanges (Figs 10–12) which can almost contact distally although there usually is a distinct gap. The flanges are also visible in a specimen from the Northern Territory (Johnson, 1964, pl.15). This contrasts with the very widely separated pterygoid hamuli, without flanges, in SE Asian specimens (Owen, 1866; Anderson, 1879; Pilleri & Gihr, 1973-1974).

The mastoid portion of the squamosal is well-developed both ventrally and laterally. Ventrally, there is a mastoid pad for attachment of the tympanoperiotic bones (Fig. 11; Owen, 1866, pl. 9, fig. 3; Anderson, 1879, pl. 42, fig. 3) and a conspicuous groove for the external auditory meatus. Laterally, the large lateral rugose mastoid portion of the zygomatic arch may reflect a broad attachment base for the sternomastoid muscles, possibly associated with flexibility of the head. The zygomatic arch of the squamosal is thus well-developed, and intermediate between *Monodon* and *Delphinapterus* on the one hand and phocoenids & delphinids on the other. Thus, contrary to Heyning (1989), *Orcaella* does not show extreme reduction of the zygomatic arch. This reduction of the arch was the only synapomorphy listed by Heyning (1989) for the clade Phocoenidae-Delphinidae. The taxonomic significance of the well-developed arch in *Orcaella* is considered as part of a cladistic analysis of the delphinoid taxa, but note that a relatively well-

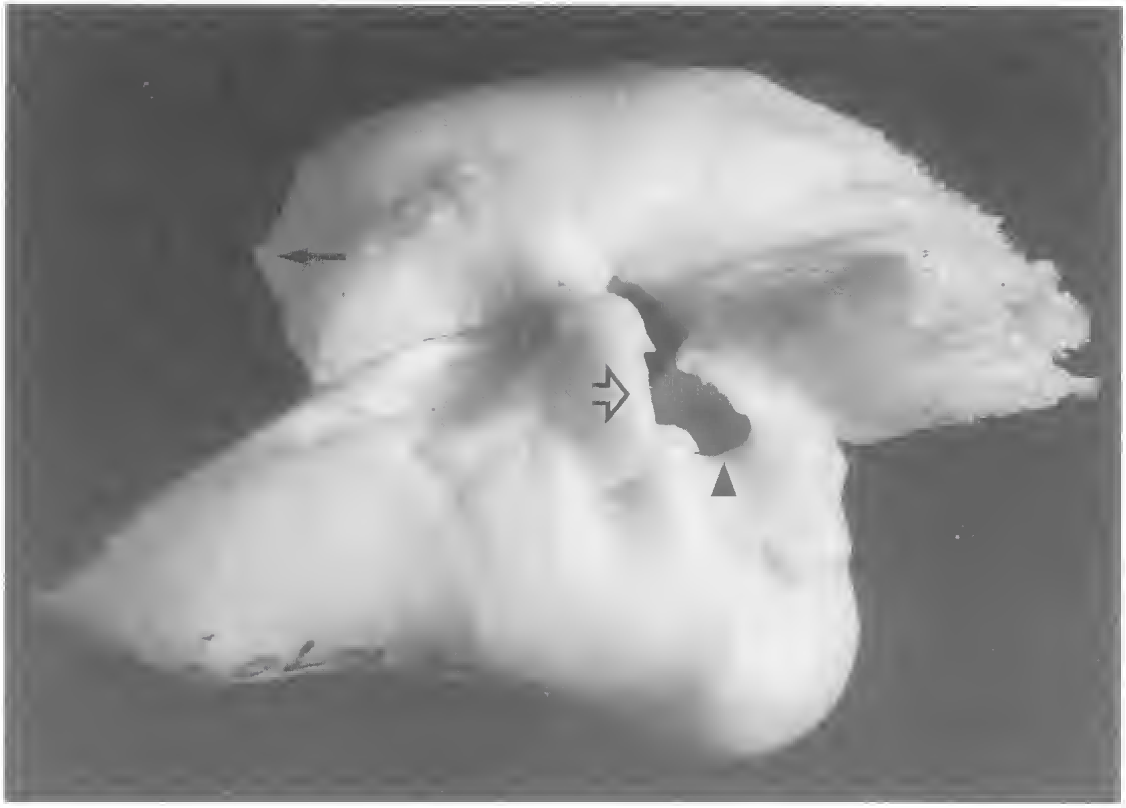

FIG. 18. Lateral view of left tympanoperiotic bones, QMJM4709. Note anterior spine of bulla; posterolateral orientation of posterior processes of bulla and periotic (directed towards viewer); triangular depression in front of sigmoid process (open arrow); posterior branch of lower tympanic aperture (triangle); concave ventral margin of bulla, and tubercle on anterior process of periotic (arrow).

developed arch also occurs in *Neophocaena*, within the Phocoenidae (pers. obs.) and in the delphinid *Orcinus* (Heyning, 1989).

The deep, elongate pit between the squamosal and parietal (Fig.11) has been noted by de Muizon (in press) in 'some delphinids'; it occurs in *Sousa chinensis* and in several delphinids (Perrin pers. comm.). It appears to be the channel for a blood vessel which exits on the back of the braincase, between the squamosal and parietal.

CONCLUSIONS. Neotenic features of the skull roof in *Orcaella* include the retained dorsal exposure of the interparietal and dorsal extensions of the parietals, poorly developed telescoping of the skull with large exposure of the frontal bones, and weak development of the mesethmoid plate on the anterior of the cranium (the last character possibly restricted to Australian animals). The relatively large braincase and short rostrum, which substantially affect the appearance of the skull, may also be neotenic features. Retention of juvenile features in *Orcaella* may compromise attempts to establish relationships based on the comparisons of its skull with adults of other genera; it would be more appropriate to compare it with juveniles of other odontocetes. However, juvenile skulls of various genera are very similar with diagnostic features often only well expressed in adults.

The basicranium may be less subject to neoteny. The skull base of *Orcaella* resembles that of *Pseudorca*, *Globicephala*, *Feresa* and *Grampus* (we have not been able to examine in detail skulls of *Orcinus*). In particular, there is a similar excavation of the palatines by the pterygoid hamuli, which can lead to separation of the medial and lateral lobes of the palatine (shared with *Feresa*, *Globicephala* and *Grampus*); posterior extension of the lateral lobe of the palatine (shared with *Globicephala*, *Feresa*, *Pseudorca*) and a transverse widening of the skull

FIG. 19. Ventral view of left bulla, QMJM4709. Note swollen outer posterior prominence (open arrow); deep interprominential notch (arrow); spongy bone along midline of bulla; posterolateral orientation of and spongy bone distally on posterior process.

FIG. 20. Ventral view of left bulla, QMJM4700. Note angulate inner posterior prominence (triangle); deep interprominential notch; posterolateral orientation of posterior process (arrow).

(as in *Pseudorca*, *Globicephala*). However excavation of the palatines and orientation of the posterior wings of the lateral palatines may be more similar to juveniles of genera such as *Globicephala* than to adults (i.e. may be neotenous). The cranial sinuses also align *Orcaella* with the bulbous-snouted dolphins (Fraser & Purves, 1962). However, in all these genera the cranial sinuses show few specializations; they may be linked by shared primitive features. A prominent feature is the well-developed zygomatic arch of the squamosal and ventral attachment of the tympanoperiotic bones which sets *Orcaella* apart from delphinids although the arch is similarly developed in *Neophocaena*.

Taxonomic utility of basicranial features needs to be examined further. It has generally proved impossible to demonstrate whether a feature is neotenic or in a generalised, unspecialised state. One option is to compare a wider range of juvenile delphinid genera than was available to us in this study. Another option is to assess polarity of basicranial features, based on outgroup analyses involving criteria other than cranial morphology. We present such analyses later in this paper.

TYMPANOPERIOTIC BONES
(Table 1; Fig.17; Appendix 1)

TYMPANIC BULLA. Standard length 34.8mm (33.0-36.5). The anterior tip can be drawn out into a spine-like process (Figs 18, 30). The outer posterior prominence is swollen and hemispherical, with no lateral compression (Fig. 19). The inner posterior prominence is sharply angulate (Figs 20, 21); a weak ventral keel extends more than half way to the tip (Fig 20). The interprominential notch is deep (Figs 19,20). There is

FIG. 21. Dorsal view of left bulla, QMJM4700. Note angulate inner posterior prominence (triangle); prominent accessory ossicle (arrow); ridges and grooves of articular facet (open arrow) which is directed posteriorly (associated with posterior orientation of periotic process).

no median furrow. A spongy, weakly developed ridge extends along the anteromedial border of the interprominential notch, continuing forward to the tip along the midline (Fig. 19). There is no compression: the width of bulla at the level of the sigmoid process is 57.8 (53.9–61.0)% of standard length. The posterior process is well developed, variable in direction from almost posterior to distinctly posterolateral. The mean angle of the lateral margin is 34.9° (17°–47.5° to long axis of bulla) (Figs 18-20). Although the articular facet with the periotic can be more posteriorly oriented (Fig. 21), the posterior process is usually obliquely oriented laterally (Figs 19,26). Distally the posterior process consists of spongy bone (Fig. 19). The facet with the posterior process of the periotic is ridged and grooved (Fig. 21).

In lateral view, the ventral margin is slightly concave (Fig. 18). A deep triangular area anterior to the sigmoid process is bounded on its ventral side by a low, wide ridge which gives rise on its anterior margin to a shallow vertical groove (Fig. 18). The accessory ossicle is prominent (Fig. 21). In medial view, the border of the involucrum is low, not rising anteriorly to form a distinctly curved margin (Fig. 22). The elliptical foramen is closed, but minute perforations are often present in the area usually occupied by the foramen (Fig. 23).

PERIOTIC BONE

DORSAL ASPECT. Standard length 35.7mm (31.0–38.2). Anterior, superior and posterior processes are in a straight line (Fig. 24). The superior process can be directed medially as a shelf of spongy bone, partially hiding the tractus spiralis foraminosus and completely obscuring the internal aperture of the aquaeductus Fallopi (canal for facial nerve) (Fig. 24). A similar medially directed shelf of spongy bone can cover the aperture of the aquaeductus cochleae and aquaeductus vestibuli (ductus endolymphaticus) (Fig. 25). The aquaeductus vestibuli is set at the base of a large funnel-shaped depression bounded by spongy bone (Figs 24,25). The tractus spiralis foraminosus is prominent (Fig. 25). The aquaeductus Fallopi is directed anteriorly at the level of the anteriomost margin of the tractus spiralis foraminosus (Fig. 25). The foramen singulare is at the posterior margin of the tractus spiralis foraminosus and separated from the aquaeductus Fallopi by a long, obliquely oriented crista transversa which has a secondary ridge continuing along the anterior margin of the fundus of the internal auditory meatus.

The posterior process forms an acute backwardly pointing triangle in dorsal view (Figs 24,26; Tables 2,3). At its maximum extent it covers only about 0.75 of the posterior process of the tympanic bulla, and tapers to a tip on the posteromedial side of the process of the bulla (Fig. 26).

LATERAL ASPECT. In external view, the anterior process is square and truncate, directed ventrally where it fuses with the bulla between the accessory ossicle and the sigmoid process (Figs 18,27). A distinct tubercle occurs on the upper half of its anterior face, near the level of the anterior margin of the cochlear portion of the periotic (Figs 18,25).

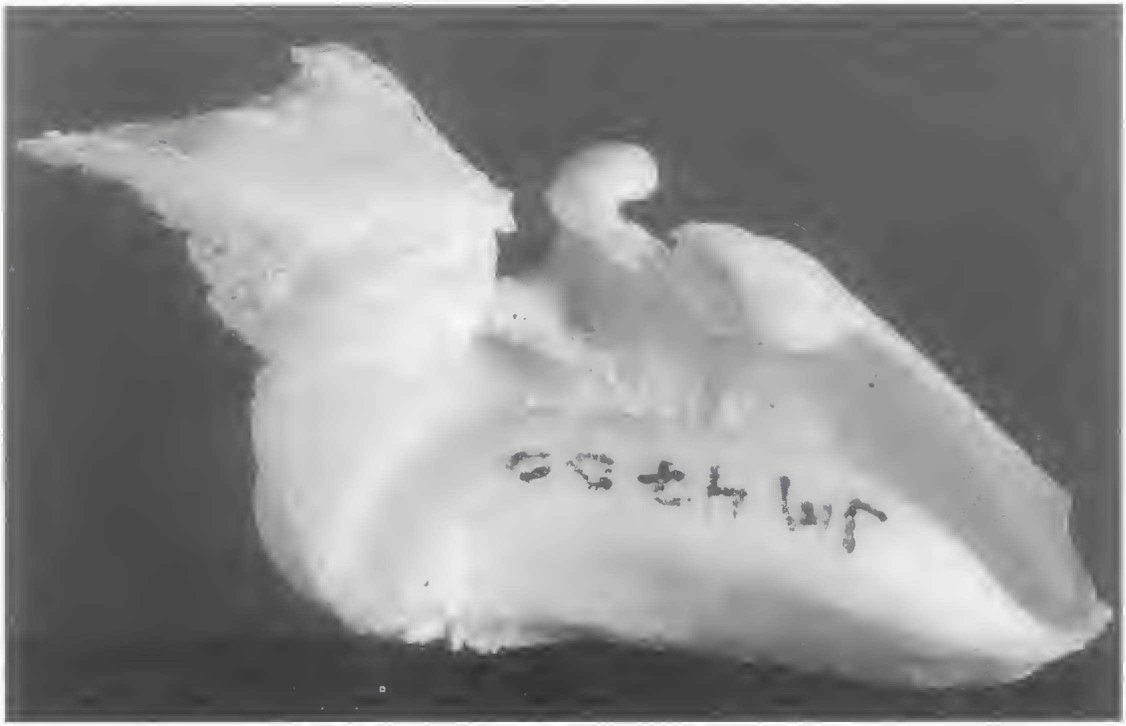

FIG. 22. Medial view of left bulla, QMJM4700. Note low medial margin of involucrum, not raised anteriorly to form sinusoidal border.

The posterior process bends sharply ventrad, to fuse with the posterior process of the tympanic bulla (Fig. 27). The distal half of the external surface of the posterior process, where it articulates with the squamosal, is spongy bone (Figs 24,26).

In medial view the periotic is oriented obliquely ventrad and is closely apposed to the involucrum of the bulla, although never touching (Fig. 25). The apertures of the aquaeductus vestibuli and aquaeductus cochleae are directed medially, that of the aquaeductus Fallopi anteromedially. The groove for the stapedius muscle is prominent (Fig. 28).

VENTRAL ASPECT. The greatest diameter of the cochlear portion is at right angles to the main axis of the periotic (Fig. 28). On the posteromedial quadrat of the cochlea is an oblique groove which runs obliquely anterior (Fig. 28). It occurs where the periotic is closely apposed to the bulla and may be a channel for a blood vessel (possibly associated with corpus cavernosum; note vascularisation of the region in Fig. 33). The anterior-posterior length of the articular facet (including the basal smooth portion (Fig. 28) and distal spongy portion) is 47.7–54.1% of the periotic length(n=5).

ARTICULATION OF PERIOTIC AND TYMPANIC BONES. In posterior view, the articulation of the posterior process of the periotic with that of the tympanic is irregular (Fig. 23). The facet for attachment with the mastoid portion of the squamosal is entirely spongy bone (Figs 29,30). Anteriorly, the articulation is between a triangular wedge of the periotic and the squamosal. Posteriorly, the connection is between the the squamosal and the posterior half of the posterior process of the tympanic bone (Figs 23,26).

DISCUSSION

COMPARISONS OF VALUES WITH KASUYA (1973). The morphometrics of this series (Table 1, Appendix 1) generally confirm values presented by Kasuya, based on specimens from unspecified localities held at the United States National Museum and Zoological Survey of India. The bulla is wider across the posterior processes in Queensland specimens. There is a

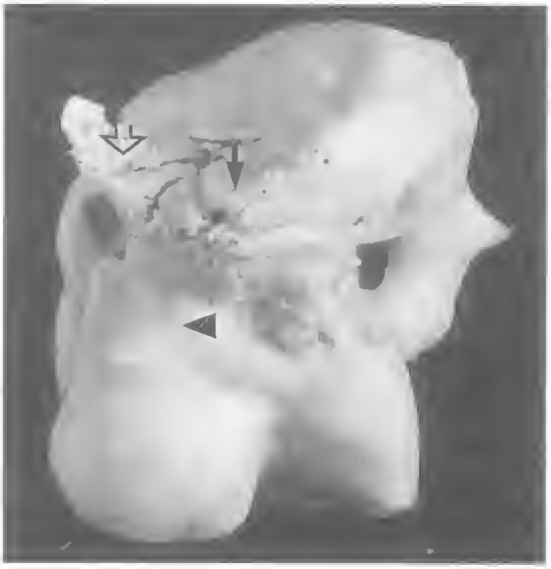

FIG. 23. Posterior view of left tympanoperiotic bones, QMJM4709. Note irregular margin of posterior processes of bulla and periotic; closed elliptical foramen, with a few pores visible (triangle). The open arrow and closed arrow indicate spongy bone of bulla and periotic respectively, which articulates with the mastoid portion of the zygomatic arch.

major discrepancy in the depth of the interprominential notch (mean=30.3 in present series vs 11.7 reported by Kasuya). This must involve a difference in measuring technique but the interprominential notch is deep in our specimens (Figs 19, 20). Our value for height of the bulla, from sigmoid process to ventral keel, is higher than reported by Kasuya (1973). His measurement was taken obliquely and incorporated not only height but also width of the bulla. Since the latter is wider in our material than reported by Kasuya, our values for 'height' should also be greater.

TAXONOMIC CHARACTERS OF THE TYMPANOPERIOTIC BONES. Characters used by Kasuya to differentiate the families of delphinoid odontocetes (Table 4) are considered for *Orcaella*: (1) direction of posterior process of bulla. This is not usually posterior as in *Delphinapterus* and the phocoenids, but variable from almost posterior to posterolateral (Figs 19,20), with a mean angle along the lateral margin of approximately 35°. Although the apex of the process is directed posteriorly, the lateral margin is always deflected and the articular facet is usually distinctly posterolateral (Fig. 19). The mean angle of deflection of the posterior process is comparable to the deflection in delphinids such as *Sousa chinensis* (e.g. 33°, 36.5° in MM1020). The greater variability in the orientation of the posterior process in our series of *Orcaella* brings into question its usefulness as a character to separate families. As such, it weakens the case for linking *Orcaella* and *Delphinapterus* in the Delphinapteridae.

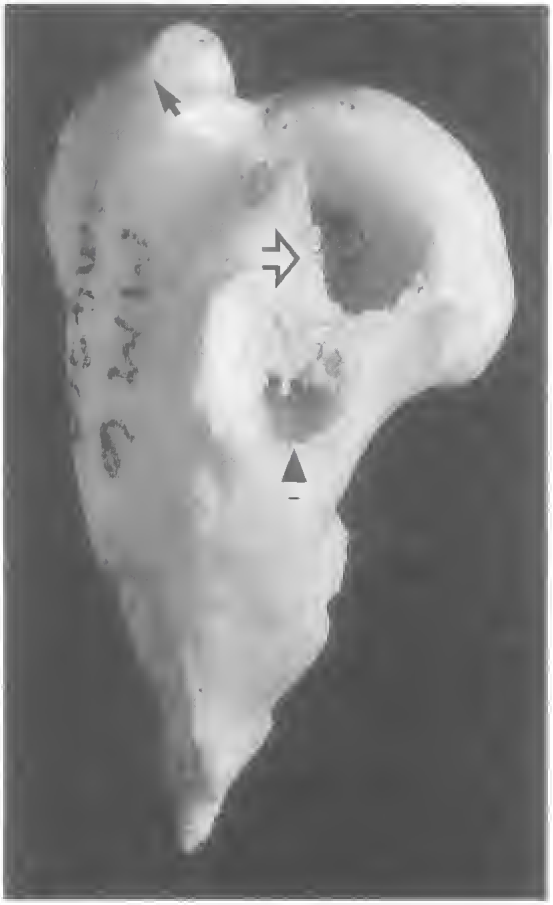

FIG. 24. Dorsal view of left periotic, QMJM4700. Note that anterior (arrow), superior and posterior processes are in line and that the latter is posteriorly directed. Note spongy bone shelf overarching the tractus spiralis foraminosus (open arrow), and wide funnel-like depression, surrounded by spongy bone, which contains the aquaeductus vestibuli (triangle).

(2) direction of posterior process of periotic. This is directed posteriorly, but the posterior orientation is found not only in *Delphinapterus* but also in phocoenids.

(3) width of posterior branch of lower aperture of tympanic membrane (LTA). Even with our larger series of specimens, there is no overlap in

TABLE 4. Tympanoperiotic characters used by Kasuya (1973) to classify odontocetes. Families are as given by Kasuya (1973). Unless otherwise stated, data for *Orcaella* are from this study; values for other species are from Kasuya (1973).

	Monodontidae *Monodon*	Delphinidae	Delphinapteridae *Delphinapterus*	Phocoenidae	*Orcaella*
direction of posterior process tympanic bulla	lateral	posterolateral to lateral	posterior	posterior	variable, mean = 35° (17°-48°)(this paper)
direction of posterior process of periotic	lateral	posterolateral to lateral	posterior	posterior	posterior
width of posterior branch of lower tympanic aperture	mean = 7.5	means from 2.5 (*Stenella attennuata*) to 7.2 (*Tursiops* cf *gilli*)	mean = 10.8 (10.1 - 11.8)	*Neophocaena* 10.3; *Phocoena* 7.5, 10.6, 10.3; *Phocoenoides* 8.9,10.5	mean = 6.5 (5.4 - 8.9) (this paper)
facet of posterior processes of bulla and periotic	ridged (this paper)	ridged (Yamada in Kasuya 1973)	ridged	smooth	ridged (this paper)
compression of bulla	strongly compressed 39.6 (37.5-41.4)	strongly compressed in *Globicephala* & *Grampus*	not compressed mean = 58.9 (58.0-59.0)	not compressed	not compressed mean = 57.8 (53.9-61.0)
ventral keel	well developed	well developed in Globicephalinae (*sensu* Kasuya)	low	low (in *Phocoena*) to well developed (in *Neophocaena, Phocoenoides*)	low
interprominential notch depth	mean = 13.9	mean =10.0 (*Globicephala*) to 16.6 (*Lissodelphis*)	mean=15.1	*Neophocaena* mean=14.1; *Phocoena* mean=14.6, 16.2 *Phocoenoides* mean=17.0, 17.6	mean=11.7 (Kasuya)
anterior spine of tympanic bulla	present	variable, present in *Globicephalinae*	absent	absent	may be present (this paper)
medial margin of involucrum	strongly sinusoidal, high anteriorly	sinusoidal, esp in Globicephalinae	sinusoidal	low, most anterior height in *Neophocaena*	low throughout
elliptical foramen	closed	open in Delphininae,closed in *Globicephala Grampus,Orcinus, Sousa,Sotalia Cephalorhynchus*	closed	closed	closed

ranges of values between *Orcaella* (LTA: 5.3–8.9%) and *Delphinapterus* (LTA: 10.1-11.8%: Kasuya, 1973). This character thus offers no support for linking *Orcaella* and *Delphinapterus* in the Delphinapteridae. Rather, the values for *Orcaella* overlap with both *Monodon* (mean = 7.5%: Kasuya, 1973: Appendix 2) and at least some of the delphinids, such as *Tursiops* (2.2–9.2%: Kasuya, 1973) and *Sousa* (7.3% : Kasuya, 1973). The LTA is wide in *Delphinapterus* and phocoenids where the posterior process of the tympanic is oriented posteriorly. If there is a lateral shift of the process, this must impinge on the LTA which is just anterior to the process. Thus one could expect a narrow LTA in taxa where the posterior process has shifted laterally; this is as observed. Characters (1) and (3) may thus be linked.

(4) articular facets of posterior processes. These are ridged in *Orcaella* but this is also true in delphinids and *Monodon*, as well as *Delphinapterus*.

(5) compression of bulla. When the width/length ratio was 0.5 or less, Kasuya (1973, fig.75) considered the bulla to show strong lateral compression. Within the Delphinidae of Kasuya, there are genera (e.g. *Globicephala*, *Grampus*) which showed strong compression, while others showed no compression of the bulla. Thus the strong compression of the bulla in *Monodon* but not in *Delphinapterus* can not be used to separate them at family level.

(6) development of ventral keel. Kasuya

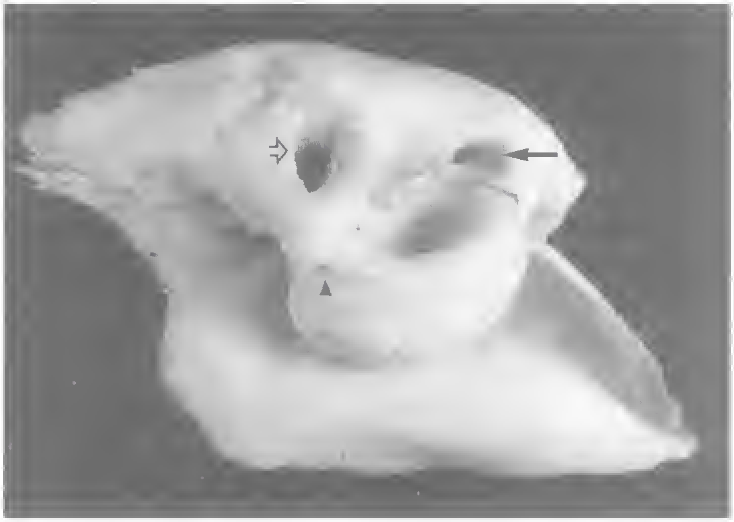

FIG. 25. Medial view of left tympanoperiotic bones, QMJM4709. Note spongy bone over cF (arrow) and Av (open arrow); position of Ac (triangles); large tractus spiralis foraminosus; tubercle on anterior process of the periotic; close association of cochlear portion of the periotic with medial porion of the bulla.

(1973:54) noted that the development of the ventral keel and the median furrow could be linked with the extent of compression of the bulla. This may also apply to the width of the interprominential notch. To the extent that these characters are linked to compression of the bulla, they can not be considered valid family characters.

(7) medial margin of involucrum. The margin is low throughout in *Orcaella*, which contrasts with the sinusoidal form of *Monodon*, *Delphinapterus* and most delphinids.

The other characters in Table 4 either vary widely within a single family (e.g. closure of elliptical foramen) or are found among several families (anterior spine of bulla) and thus are of limited use in defining families.

PERIOTIC TRIANGLE. Pilleri et al. (1989) defined the periotic triangle, which is formed by connecting the apertures of the canal for the facial nerve (aquaeductus Fallopi), aquaeductus vestibuli and aquaeductus cochleae. They recognized 6 types, including a monodontid triangle in *Monodon*, *Delphinapterus* and *Orcaella*. The monodontid triangle was defined by (1) apertures of aquaeductus cochleae and aquaeductus vestibuli 'roughly at' the same level, hence angle alpha almost a right angle triangle; (2) distance between the two apertures (AvAc) roughly equal to that between the aquaeductus vestibuli and canal for facial nerve (AvcF); and (3) angles beta and gamma approximately equal (i.e. 45°).

Considering each character of the monodontid triangle:

(1) alpha almost a right angle This was only approximately so for *Delphinapterus* (108°: Pilleri et al., 1989), but more so for *Monodon* (99°,90°,90° Pilleri et al., 1989) and for *Orcaella* (mean=85.4° (72°-102°); Pilleri et al., 1989:

FIG. 26. Dorsal view of left tympanoperiotic bones, QMJM4709. Note posterior orientation of posterior process of periotic; posterolateral orientation of posterior process of tympanic and expanse of spongy bone (arrow) which articulates with the zygomatic arch .

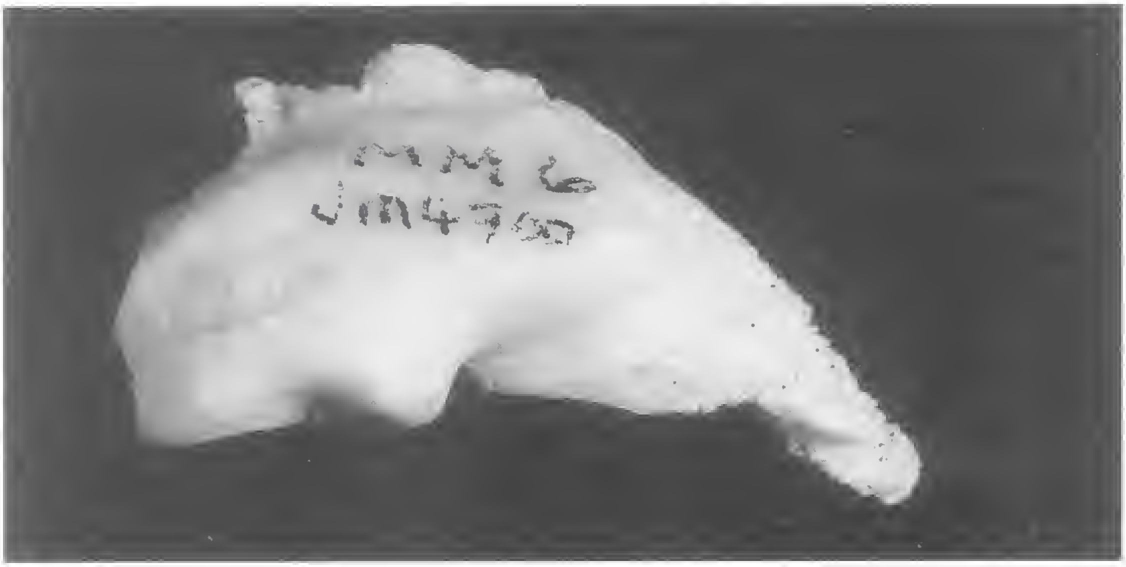

FIG. 27. Lateral view of left periotic, QMJM4700. Note squared off form of anterior process (to the left); ventral deflexion of posterior process to form triangular wedge resting on top of posterior process of tympanic.

86°,84°). However the 'delphinid triangle' is approximately a right angle; the mean value of alpha from Pilleri et al. (1989) for *Monodon* and *Delphinapterus* was 96.8° vs 97.1° for delphinids.

(2) AvAc approximately equal to AvcF, thus AvAc/AvcF approximately equal to 1.0. We had to calculate these figures for *Delphinapterus* and *Monodon* from Pilleri et al. (1989, fig.34). The line from AvAc was equal to that from AvcF in *Delphinapterus* and was about 0.8 of the length of AvcF in *Monodon*. Based on 15 measurements in our series, the line AvAc was about 0.70 (mean=0.73) the length of AvcF, which cannot be considered 'approximately equal'. In our study, there is considerable variation between observers, with the means for two sets of observations as 0.68 (n=10) and 0.82 (n=5); moreover, the range is large (from 0.54-1.00 in the first series; 0.70-0.92 in the second). In defining the 'delphinid' triangle, Pilleri et al. (1989) stated that the line Ac-Av is 'less' than Av-cF. Given the unclear boundaries contrasting this statistic for the 'monodontid' and 'delphinid' triangle,

FIG. 28. Ventral view of left periotic, QMJM4700. Note strong ventral deflexion of anterior process (upper right); great transverse width of cochlear portion; oblique groove on postero-medial border of cochlear portion (open arrow); fenestra ovalis (triangle); prominent groove for stapedial muscle, running obliquely below fenestra ovalis; ridged, compact basal portion of posterior process (arrow).

FIG. 29. Oblique ventral view of skull, QMJM4720, incompletely cleaned. Connective tissue (broad arrow) holds tympanoperiotic bones in original, ventral position against mastoid pad (open arrow) of zygomatic arch. Also note falciform process of the zygomatic arch (triangle).

and the extensive variability within *Orcaella*, the ratio AvAc/AvcF must be interpreted with caution.

(3) beta and gamma roughly equal; i.e. gamma /beta about 1.0. In measuring periotics of 9 animals, variability and observer bias were extensive. Our mean values (beta 58.3 (47–70); gamma 36.3 (30-54) correspond closely to those of Pilleri et al. (1989): beta 61,62; gamma 33,34. The mean value for beta was much larger than that given by Pilleri et al. (1989) for monodontids (mean=49.5) and delphinids (mean=54.7). The value for gamma was intermediate between that for monodontids (41.9) and delphinids (28.2) (Pilleri et al., 1989, table 16). Given the wide overlap in values (e.g. gamma: *Orcaella* 30-54, *Delphinapterus* and *Monodon* 32-48, delphinids 18-38) the data provide equivocal support for a relationship between *Orcaella* and monodontids.

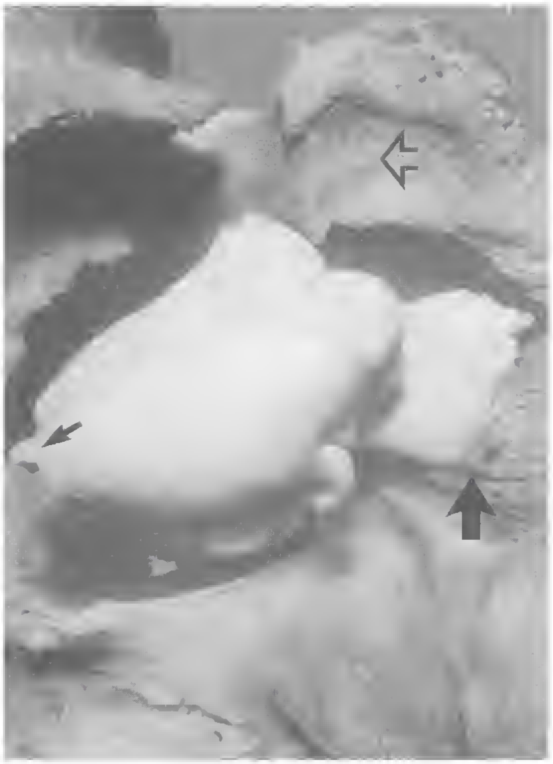

FIG. 30. Oblique ventral view of skull, QMJM4714, with tympanoperiotic bones re-attached against mastoid pad (broad arrow) of zygomatic arch. Note anterior spine of bulla (small arrow); ventral deflexion of paroccipital process of exoccipital, with shallow depression on anterior face (open arrow), and falciform process flattened against the skull base.

The mean of gamma/beta for *Delphinapterus* and *Monodon* is 1.01 (Pilleri et al. (1989)), but our mean for *Orcaella* is 0.64 (n=16). The ratios from Pilleri et al. (1989) are even lower (0.54, 0.55). Again, there is considerable variation within and between observers in our specimens (1st series mean=0.59 (0.43–1.00, n=11); 2nd series mean=0.78 (0.60–0.92, n=5)). However neither our series nor that of Pilleri et al. (1989) can be considered ‘approximately the same’.

Variability in monodontid triangle values seem extensive even for *Delphinapterus* and *Monodon*, but our figures and those of Pilleri et al. (1989) for *Orcaella* correspond only poorly to the definition of the monodontid triangle. The closest correspondence is in the angle alpha (mean=85.4° for *Orcaella*, which approximates 90°). However the delphinid triangle is also approximately 90°.

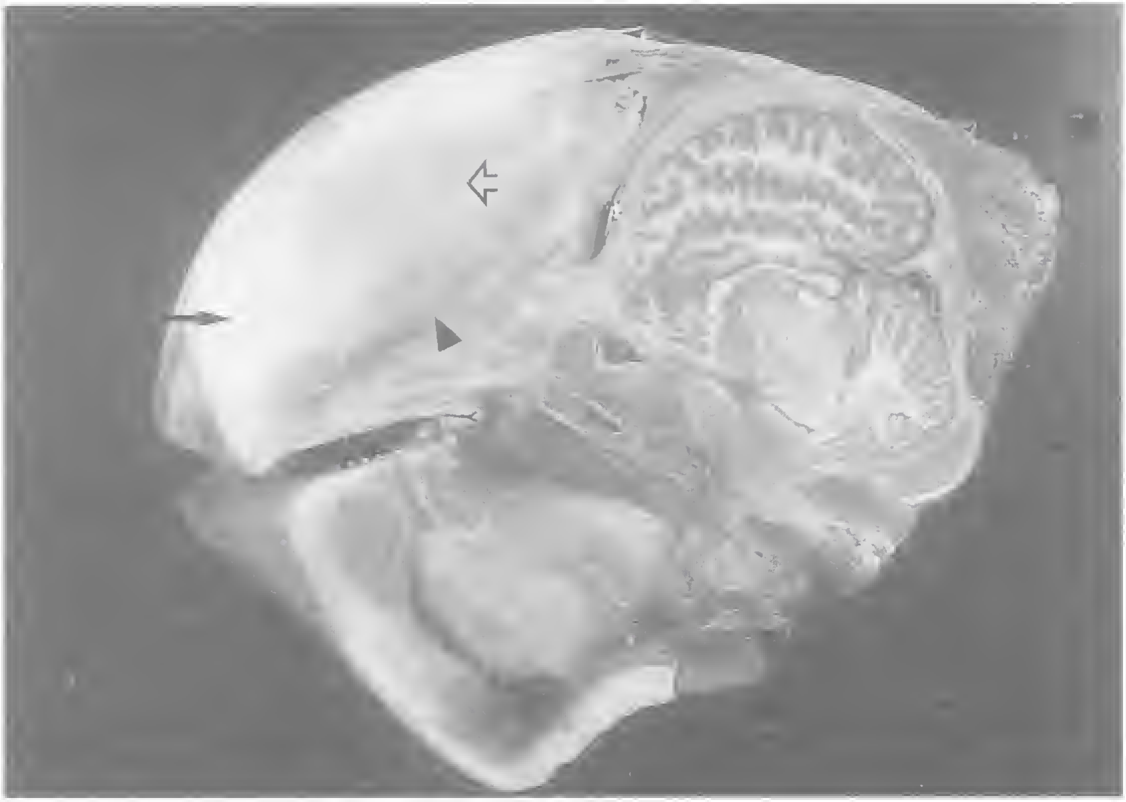

FIG. 31. Near sagittal section of head, MM334, a 1.86m ♀. Note moderate development of melon (open arrow), prominent rostral muscles (triangle), and extent of connective tissue (arrow) at the front of the upper jaw.

Evidence from the so-called monodontid triangle that *Orcaella* is closely related to either *Delphinapterus* or *Monodon* is equivocal at best.

ADDITIONAL CHARACTERS OF PERIOTIC BONES. Details of the tractus spiralis foraminosus, such as a prominent crista transversa, resemble *Neophocaena* and *Pontoporia* (Perrin pers. comm.). The groove in the periotic, which may be the impression of a blood vessel (Fig. 33), has not been described in other odontocetes, and thus can not be used as a taxonomic-character.

ATTACHMENT OF TYMPANOPERIOTIC TO SQUAMOSAL. Kasuya (1973) and Kleinenberg et al. (1969) noted that the periotic of the beluga was firmly sutured to the squamosal; this was considered characteristic of *Delphinapterus* and *Monodon* by Tomilin (1967). Heyning (1989) did not find the periotic sutured to the squamosal in beluga he examined nor is it sutured in beluga and narwhal examined by one of us (PA). Kasuya (1973) described how the dorsal surface of the periotic is grooved to articulate with the squamosal. We could not confirm the type of articulation in beluga and it is not evident in published photographs where the tympanoperiotics seem to have been re-attached in a variety of orientations. In a juvenile narwhal (UBC9467) the periotic is attached to the squamosal by a thin wedge of the posterior process bounded ventrally by the posterior process of the tympanic. In narwhal and beluga, the main attachment seems to be by the periotic, while in *Orcaella* the attachment is shared between the tympanic and the periotic. The attachment in all three genera appears to be by connective tissue on a mastoid pad on the ventral side of the zygomatic arch within a large postglenoid space (Figs 29,30); this contrasts with phocoenids and delphinids where the attachment is in a cavity formed by the squamosal, exoccipital and basioccipital (Kasuya 1973; pers. obs.).

Ventral attachment of the tympanoperiotics offers the most convincing evidence that *Orcaella*

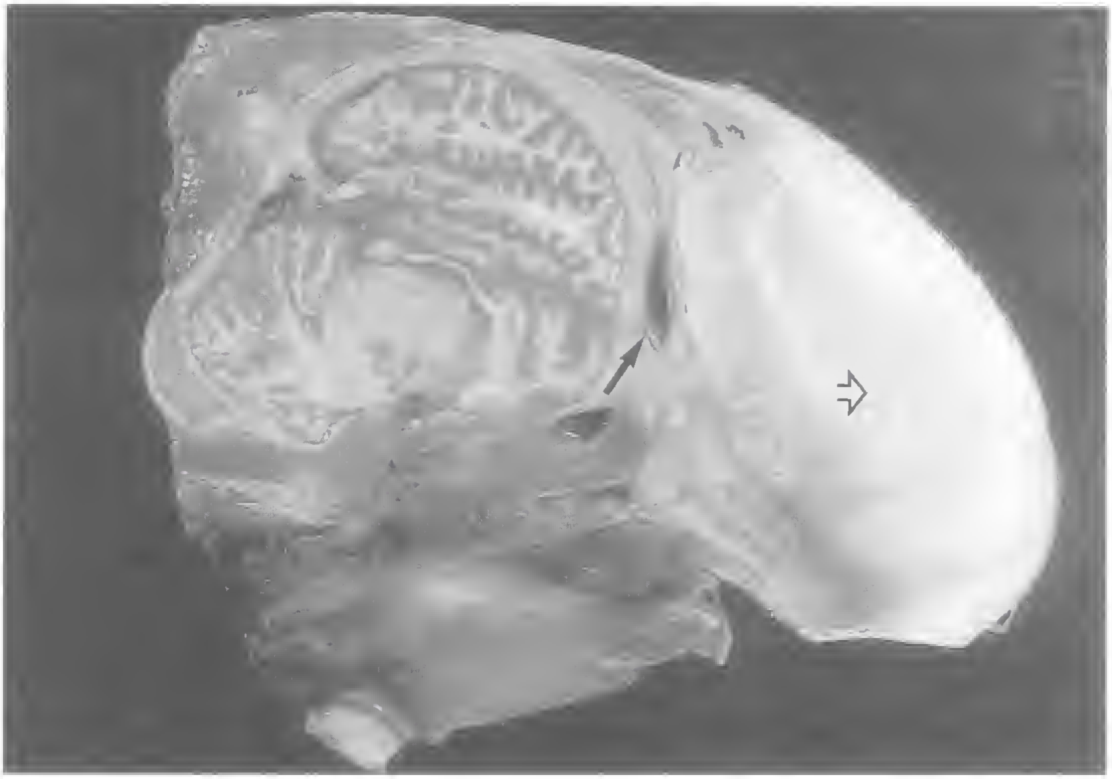

FIG. 32. Opposing section to that in Fig. 31, showing development of melon (open arrow), connective tissue and rostral muscles. Also note partial section of the inferior nares (arrow).

may be related to *Delphinapterus* but the feature is shared with *Monodon* (placed in a separate family by Kasuya) and may be a primitive feature.

CONCLUSIONS. 1. Orientation of the posterior process of the tympanic bulla is variable in *Orcaella*, but the lateral margin is usually deflected approximately 35° from the main axis of the bulla. The deflection of the process is more comparable to delphinids such as *Sousa* than to *Delphinapterus*. A larger series of measurements for the posterior branch of the lower aperture of the tympanic membrane shows that, contrary to Kasuya (1973), it is within the range of delphinids rather than that of beluga. These findings weaken arguments for beluga and *Orcaella* being cofamilial. The other characters (Table 4) provide equivocal evidence for the Delphinapteridae.

2. Linking *Monodon*, *Delphinapterus* and *Orcaella* in one family is inconsistent. Including *Monodon* and *Delphinapterus* in one family implicitly rejects the orientation of the posterior processes of the bulla and periotic, the compression of the bulla and the width of the posterior branch of the lower tympanic aperture (LTA) as family characters, since they differ between the two genera. However, orientation of the posterior processes and width of the LTA were the main characters used by Kasuya (1973) to unite *Orcaella* and *Delphinapterus* in the Delphinapteridae.

3. Our data and that of Pilleri et al. (1989) on the periotic triangle provide either no support or only equivocal support for linking *Orcaella* with either *Delphinapterus* or *Monodon*.

4. Tympanoperiotics of *Orcaella* are attached by connective tissue to a prominent mastoid pad on the ventral surface of the zygomatic process. A similar ventral connection occurs in *Delphinapterus* and *Monodon*, although there appears to be a greater involvement of the posterior process of the tympanic bulla in the articulation of *Orcaella*. In phocoenids and delphinids the attachment of the posterior processes is within a cavity formed by the squamosal, exoccipital and basioccipital bones.

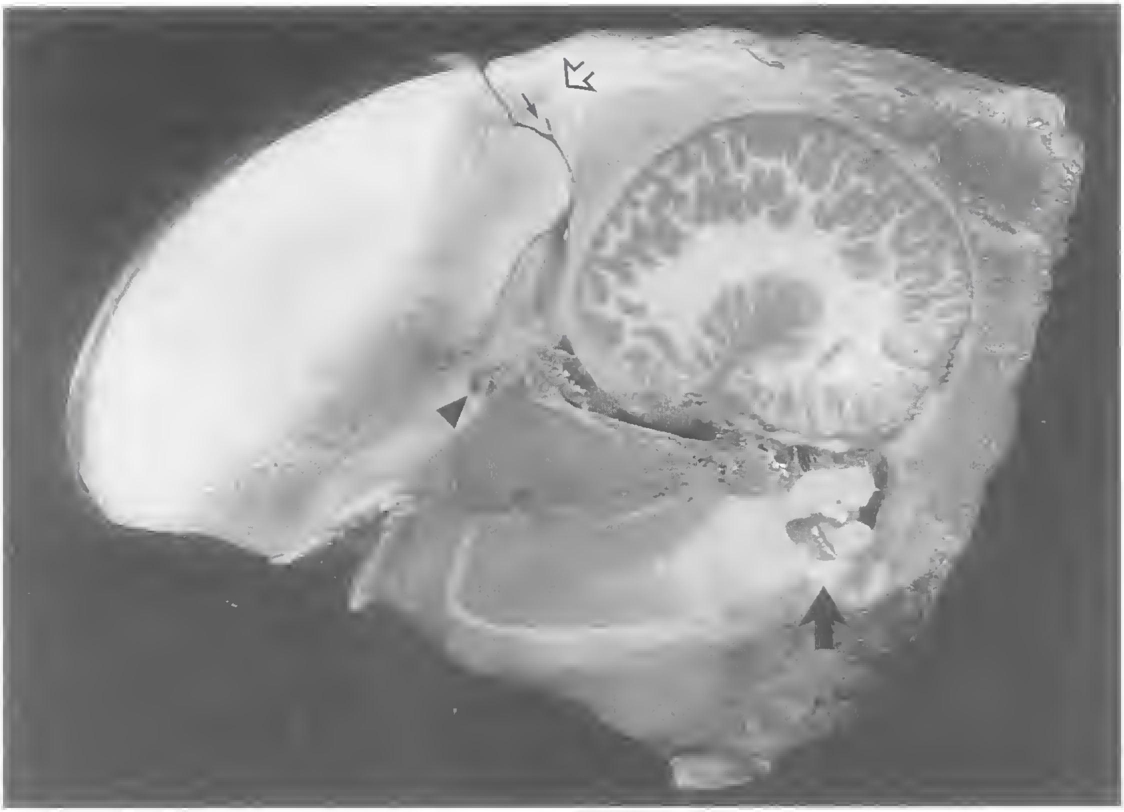

FIG. 33. Section approximately 2 cm left of Fig 32. Note well developed rostral muscles; blowhole ligament with cartilaginous inclusion (small arrow); diagonal membrane (open arrow); vascularised excavation of palatine bones (triangle); tympanoperiotic bones in cross-section (broad arrow) bordered by acoustic fat anteriorly and peribullary sinuses dorsally and posteriorly.

FACIAL ANATOMY

EXTENT OF MELON. MM333 from Mackay has a gape of 130 mm. The anterior boundary of the melon starts about 30 mm behind the tip of the upper jaw; the anterior 30 mm (or c.23% of gape length) is blubber and dense connective tissue. The melon is bordered ventrally by well-developed rostral muscles. The near sagittal sections of MM334 from Ellis Beach (Figs 31–33) show the well-developed rostral muscles and the limited extent of the melon.

Mead (1975) demonstrated that the superficially similar 'bulbous-headed' dolphins are anatomically quite distinct. For instance, *Grampus* has an extensive melon while *Pseudorca* has a preponderance of dense connective tissue in the forehead. *Orcaella* is closest to the generalized delphinid, with neither melon nor connective tissue developed to a high degree. It resembles genera such as *Lagenorhynchus* or even *Tursiops* as much as it does any of the bulbous headed species.

The bulbous shape of the forehead is one of the reasons for the supposed relationship of *Delphinapterus* and *Orcaella*. Anatomy of the forehead in these two genera is distinct, however, except perhaps for the well-developed rostral musculature (Figs 31-33 for *Orcaella*; Heyning (1989:33) for *Delphinapterus*). There is a conspicuous melon in the beluga, which runs to the front of the forehead (Pilleri et al., 1980, fig.13). The profile of the beluga's forehead is quite malleable and soft. Changes in the forehead are well documented for this species. In contrast, the anterior forehead of *Orcaella* is exclusively dense connective tissue, and it was not possible to deform the profile of the forehead in specimens we examined. Although the 'facial expression' is 'changeable' (Martin,1990), the profile of the head did not vary on captive *Orcaella* observed

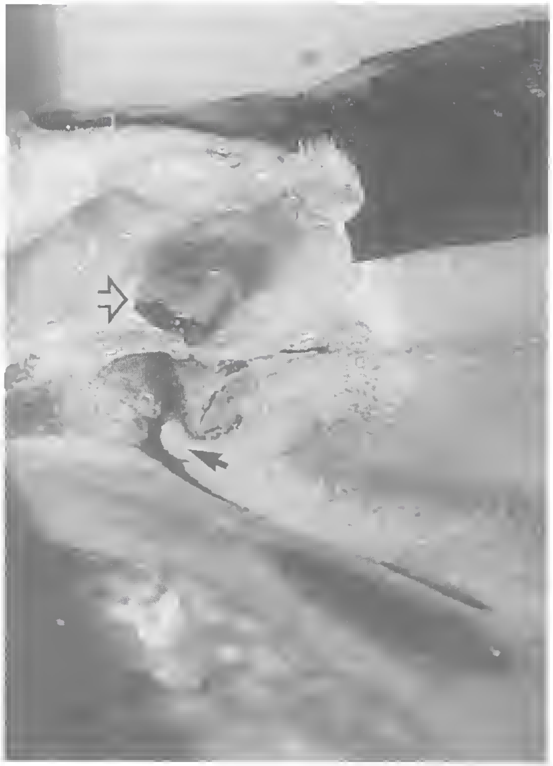

FIG. 34. Oblique dorsal view of section in Fig 32, partially dissected to reveal right vestibular sac (open arrow), with folded walls. Also note lip of the nasal plug (arrow).

FIG. 35. Enlarged view of section in Fig 31. Note muscles around nasal sacs; the darkly pigmented dorsal vestibular sac (small arrow); elongate tubular nasofrontal sac (open arrow); blowhole ligament with cartilage (broad arrow); nasal plug with prominent lip (below blowhole ligament) entering the inferior vestibule; extensive premaxillary sac (triangle).

at the Jaya Ancol Oceanarium (Dr. A. Preen pers. comm.).

Thus the resemblance between *Orcaella* and *Delphinapterus* appears superficial. There is at least as great a similarity between *Orcaella* and the phocoenid *Neophocaena*, which suggests head shape is a shared primitive character.

RESPIRATORY TRACT. The blowhole forms a crescent, with the horns directed anteriorly; its width is 1.5–2.2% of the standard body length. The blowhole is displaced towards the left in MM333, 334.

The spiracular cavity continues ventrally from the blowhole as a transverse slit, which is surrounded by dense connective tissue anterior to the vertex of the skull.

The vestibular sacs extend laterally to posterolaterally from the spiracular cavity. In MM333 they appear to be collapsed and cover less than half the area of the vestibular sacs in the larger MM334. In both specimens, however, the right and left vestibular sacs are approximately equal in size. They are lined with a darkly pigmented epithelium and the walls have slight concentric folds in MM334 (Fig.34) and MM335. The vestibular sacs are connected to the spiracular cavity by a medial ventral slit.

The nasofrontal sacs are immediately below the vestibular sacs. The anterior portion of the nasofrontal sac is tubular; in MM335 the right naso-frontal is 14mm in diameter and the left 10 mm. The anterior portion of the nasofrontal sacs bend posterolaterally, then medially to form a U-shaped tube. The lateral wall of the right nasofrontal sac has a series of perforations and trabeculae, but no extensions from the nasofrontals. The nasofrontal sacs of MM333 are collapsed, about 2.5 mm diameter for the left horn; details are not obvious. In both specimens, the nasofrontal sacs enclose an area comparable to that covered by the vestibular sacs. In MM334, the right nasofrontal sac also has trabeculae.

FIG. 36. Oblique dorsal view of section in Fig. 32. The vestibular sac has been partly removed. The dull probe marks passageway of spiracular cavity from level of vestibular sac to exit between the blowhole ligament (open arrow) and nasal plug (arrow). The pin indicates anterior portion of naso-frontal sac. The lip of the nasal plug has been drawn forward to reveal inferior vestibule. The premaxillary sac (triangle) is also more apparent due to displacement of the nasal plug. There is no indication of posterior septum of blowhole ligament nor posterior nasal sac.

Much of the anterior portion is collapsed and visible in section as a slit (Fig. 35).

In MM335, a probe could be passed from the posterior portion of the nasofrontal sac ventrally to connect with the spiracular cavity; this portion is termed the inferior vestibule (see discussion). The inferior vestibule is bounded anteriorly by the blowhole ligament, which runs laterally on both sides from the nasal septum. In the sagittal section of MM334, the inferior vestibule accommodates the lip of the nasal plug and runs behind the blowhole ligament, apparently in connection with a poorly defined posterior portion of the nasofrontal sac. A small cartilage inclusion is present in the blowhole ligament of MM334 (Figs 35,36). There is no indication of a posterior septum of the blowhole ligament (as defined by Curry, 1992) in any of the specimens examined. The cavity behind the blowhole ligament and connecting with the posterior portion of the nasofrontal sacs is not subdivided by a fold of tissue; i.e. there is no indication of a posterior nasal sac.

The prominent nasal plugs have a conspicuous lateral lip, which fits into the inferior vestibule (Figs 35,36). In MM333, these are 5 mm wide or 19% and 15% of the total width of the left and right nasal plugs respectively. The melon enters the right but not the left nasal plug.

The premaxillary sac is a thin-walled sac with darkly pigmented tissue (Figs 33,35,36). In MM335, the area of the premaxillary sacs is about double (1.7–2.1 times) that of the vestibular sacs. In MM333, in which the vestibular sacs appear collapsed, the premaxillary sacs cover an area about 5–7 times that of the vestibular sacs.

No accessory sacs were found.

Between the inferior vestibule and skull in the sagittal sections of MM334 is a distinct connective tissue sheet which appears to be the diagonal membrane (Fig. 33).

Anderson (1879) noted maxillary (=vestibular) sacs, 'naso-facial' sacs entering the common spiracular cavity and 'large' premaxillary sacs in *Orcaella brevirostris* from India. His description was not detailed enough to compare with more recent studies on the respiratory tract.

Schenkkan (1973), Mead (1975), Heyning (1989) and Heyning & Mead (1990) reviewed the variations in the upper respiratory tract and associated nasal sacs. The cladistic analysis of Heyning (1989) was especially affected by characters of the facial region (24/40 characters), with 11/40 characters referring to the respiratory tract alone. He identified the loss of the 'posterior nasal sac' as a synapomorphy for the Delphinidae. This feature needs to be considered in more detail. The inferior vestibule 'forms a communication between the spiracular cavity and the nasofrontal sac. Hence, if you have both of those features, you, by definition, have the "inferior vestibule"' (Mead pers. comm., 8.3.94). Heyning

TABLE 5. Data for cladograms.

Platanista	0—000000100011010—0100200000001000000
Pontoporia	1010100001000001010000000201000010100010
Inia	1010000000100100101000010021100000100010
Delphinapterus	1000102101100001 00—11102010111010 0111
Monodon	1000102101100001 00—10101011110110 0111
Phocoena	1101102120011001010100001011011101111111
Neophocaena	1101102120011001010100101111011101111111
Tursiops	100101211000100101101000001211100101111
Sousa	100111101000100101101000001211100101111
Globicephala	100101212000100101000000001211101101111
Orcaella	100111211000100101000010011111100100111

(1989) used the term 'posterior nasal sac' in its simplest form to refer to a dorsal extension of the inferior vestibule, as in the ziphiid *Mesoplodon* (Heyning, 1989:10). In *Berardius* and *Hyperoodon*, there is a separation of the posterior cavity into an anterior chamber which receives the nasofrontal sac and a caudal chamber which was referred to as the posterior nasal sac. The separation is by a transverse fleshy fold, the 'hintere klappe' of Kukenthal 1893 according to Heyning & Mead (1990). Curry (1992) re-described the facial anatomy of species of *Phocoena* and *Phocoenoides*, and figured a posterior nasal sac separated from the chamber receiving the nasofrontals by an extensive sheet of connective tissue which she referred to as the 'posterior septum of the blowhole ligament'. As a result of the well-developed septum, the upper respiratory tract of phocoenids is well forward of the vertex of the skull. This is shown by diagrams and photographs in Heyning (1989), Curry (1992), Reidenberg & Laitman (1987, fig. 3b) and Schenkkan (1973). This contrasts with the more posterior placement of the upper respiratory tract in delphinids which lack or have a reduced posterior septum (e.g. *Pseudorca* : Mead 1975) and lack a posterior nasal sac (Mead, 1975; Heyning, 1989). The contrast is shown well by comparing the sagittal section of *Phocoena* (Reidenberg & Laitman, 1987, fig. 3b) with *Delphinus, Grampus* and *Globicephala* (Reidenberg & Laitman, 1987, figs 2a,2b,3a), and *Orcaella* (Fig. 31).

In our *Orcaella*, the nasofrontal sacs are clearest in sagittal sections. In all specimens the tubular form of the posterior portion of the nasofrontal sac is ill-defined and there is an extensive connection between it and the inferior vestibule. In this respect, the connection is closer to that illustrated in *Tursiops* by Lawrence & Schevill (1956, fig. 20b) than to Mead's (1975) fig. 4 of the same genus. Sagittal sections of *Orcaella* (Figs 31–33) correspond closely to those in Lawrence & Schevill (1956, figs 3, 4).

Whereas the anatomy of the respiratory tract is well-documented for delphinids (Schenkkan,1973; Mead, 1975), phocoenids (Curry,1992) and ziphiids (Heyning,1989), the situation is less clear in other odontocetes, including the narwhal and beluga. For the former, the only information is a diagram (Huber,1934), which has been discussed by Mead (1975) and Heyning (1989). The occurrence of a posterior nasal sac in narwhal is based on this diagram, even though it is difficult to relate certain other details in the diagram, e.g. the 'lateral sacs' (=vestibular sacs) and the nasofrontals, to the pattern in other odontocetes. The diagrams and description of the respiratory tract of beluga by Kleinenberg et al. (1969) more clearly suggest a posterior nasal sac but again are open to interpretation. Fortunately, Heyning (1989) was able to dissect a beluga and confirmed that the 'inferior vestibule divides dorsally into a rostral nasofrontal sac and caudally into a posterior nasal sac'. The upper respiratory tract appears to be more anteriorly situated in beluga, as in *Phocoena*, if we are interpreting correctly the features in the photograph of a sagittal section (Pilleri et al., 1980, fig. 13). This is consistent with the suggestion above that the anterior position of the respiratory tract is correlated with a posterior nasal sac and well-developed posterior septum. The diagram of the head of a narwhal (Raven & Gregory,1933) also suggests that the respiratory tract is far forward, and Schenkkan (1973), based on Huber's 'very clear diagrams', noted that the blowhole and nasal tract were 'relatively more anteriorly' situated in narwhal than in other odontocetes.

The position of the nasal sacs and upper respiratory tract in our *Orcaella* is consistent with that in delphinids (Lawrence & Schevill, 1956; Mead, 1975) and contrasts strongly with the phocoenid pattern (with a well-developed posterior septum of the blowhole ligament) (Curry, 1992). The orientation of the respiratory tract is not as well documented in monodontids, but appears to be closer to phocoenids and thus differs from what we observed in *Orcaella*. Heyning (1989) noted that in the beluga, the

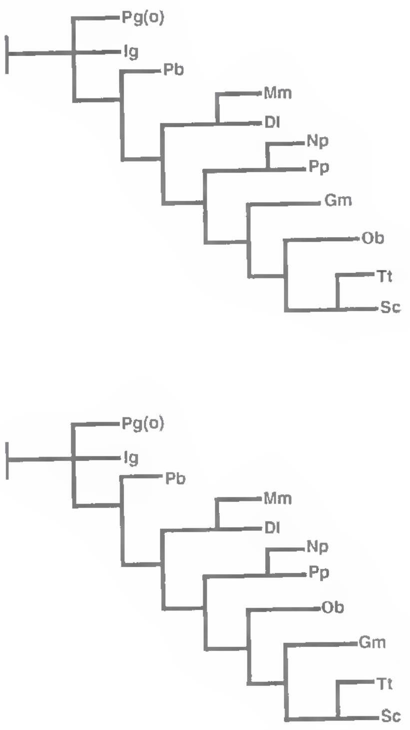

FIG. 37. Analysis One; all characters used. Cladogram length 61; consistency index 70; retention index 75. Abbreviations (for Figs 37-47) are: Pg(o): *Platanista gangetica* (outgroup); Ig: *Inia geoffrensis*; Pb: *Pontoporia blainvillei;* Mm: *Monodon monocerus*; Dl: *Delphinapterus leucas*; Np: *Neophocaena phocaenoides*; Pp: *Phocoena phocoena*; Gm: *Globicephala melas*; Ob: *Orcaella brevirostris*; Tt: *Tursiops truncatus*; Sc: *Sousa chinensis.*

vestibular sacs have apertures on the anterior aspect of the vestibule, as in phocoenids. In our *Orcaella*, the vestibular sac connects with the spiracular cavity by a transverse slit as in *Tursiops* (Lawrence & Schevill, 1956, fig. 20a). Thus, structure of the upper respiratory tract in *Orcaella* is unlike that in either beluga or narwhal.

The balance of evidence suggests that the posterior nasal sac is a feature of ziphiids, beluga & narwhal, and phocoenids but that it is lost in delphinids as indicated by Heyning (1989). This is one of the most soundly based morphological synapomorphies for the Delphinidae. Thus the apparent lack of a posterior nasal sac in *Orcaella* supports its inclusion in the Delphinidae and argues against its close relationship with *Delphinapterus*. The position of the upper respiratory tract in *Orcaella*, close to the vertex of the skull, is also consistent with the pattern in delphinids. The larger premaxillary sacs relative to vestibular sacs in *Orcaella* is similar to the pattern in delphinids (Schenkkan, 1973). 'Lateral lips on the nasal plugs' was also inferred by Schenkkan (1973) to be a specialised feature, best developed in delphinids; *Orcaella* has well-developed lateral lips on the nasal plugs. However, this feature is inadequately known in other odontocetes, including beluga and narwhal.

The form of the vestibular sacs and, more especially, trabeculae in the right nasofrontal sac of *Orcaella* resemble *Globicephala* (Mead, 1975). The trabeculae in *Globicephala* were considered 'extremely unusual' by Mead, and their occurrence in *Orcaella* and *Globicephala*, along with the bulbous head, suggests a relationship between the two genera. However, the melon structure is different and other criteria need consideration in assessing this relationship.

PHYLOGENETIC ANALYSIS
(Table 5)

RESULTS. In the first analysis all characters were used and treated as non-additive. The two cladograms produced (Fig. 37a,b) link beluga and narwhal as a sister group to *Phocoena, Neophocoena*, the delphinid genera and *Orcaella*. The latter was placed with the delphinid genera, although the two cladograms differed in detail. A comparison of ancestral states in the two cladograms was extracted by option 'hcl' of Hennig86. This shows *Orcaella* linked with *Sousa* and *Tursiops* because only the atlas and axis were fused. *Globicephala* was closer to *Phocoena* and *Neophocaena* as it has at least 3 cervical vertebrae fused. This is a weak character on which to base such a separation, but there is no a priori basis to choose between the cladograms. However, except for the position of *Orcaella* and *Globicephala*, the two cladograms are identical.

In the second analysis, mandibular symphysis length, rostrum length, fusion of cervical vertebrae, presence/absence of olecranon process, roofing of temporal region were masked through option 'cc' because they may be homoplastic. The one cladogram produced (Fig. 38) was identical to Fig. 37b.

As is general practice (Forey et al.,1992), inapplicable values were coded '-, the same as missing values. Platnick et al. (1991) cautioned that while missing and inapplicable values are treated the same computationally, they are logically different (missing values can eventually be coded as

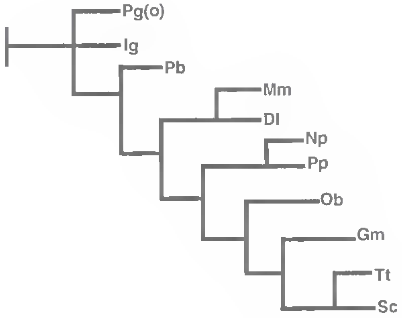

FIG. 38. Analysis 2; characters showing homoplasy masked. Cladogram length 52; consistency index 69; retention index 72.

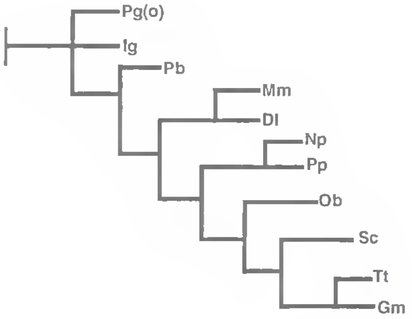

FIG. 39. Analysis 3; characters showing homoplasy and inapplicable characters masked. Cladogram length 48; consistency index 68; retention index 73.

0, 1, etc but there is no way to logically code inapplicable values). They further suggested that cladograms resolved on the basis of inapplicable values may be questionable. In our analysis, this could apply to the subdivision of the pterygoid sinuses, which is a valid character for dolphins and porpoises but inapplicable to monodontids. In analysis 3 homoplastic (as in Analysis 2) and inapplicable characters (relating to subdivision of the pterygoid sinuses) were masked.

In the single cladogram (Fig. 39), *Tursiops* and *Globicephala* were linked, with *Sousa* and *Orcaella* more distantly linked within the terminal cluster of branches. The most important feature is that *Monodon* and *Delphinapterus* were still a group distinct from *Phocoena, Neophocaena, Orcaella* and the delphinid genera. Thus, structure of the other cladograms was not being driven by inapplicable characters. The characters of the pterygoid sinuses were retained in subsequent analyses, because they do allow clearer separation of the delphinid genera without unduly affecting the major branches of the cladogram.

Polarity of a number of the characters is equivocal. In Analysis 4, the homoplastic characters (Analysis 2) and equivocal characters (orbit in front of nares, convex profile of skull, length of zygomatic arch of squamosal, disappearance of superior lamina of pterygoid, orientation of posterior process of periotic, orientation of posterior process of tympanic, form of sigmoid process, presence/-absence of lateral furrow, breadth of lower tympanic aperture, retraction of premaxillaries from nasals,

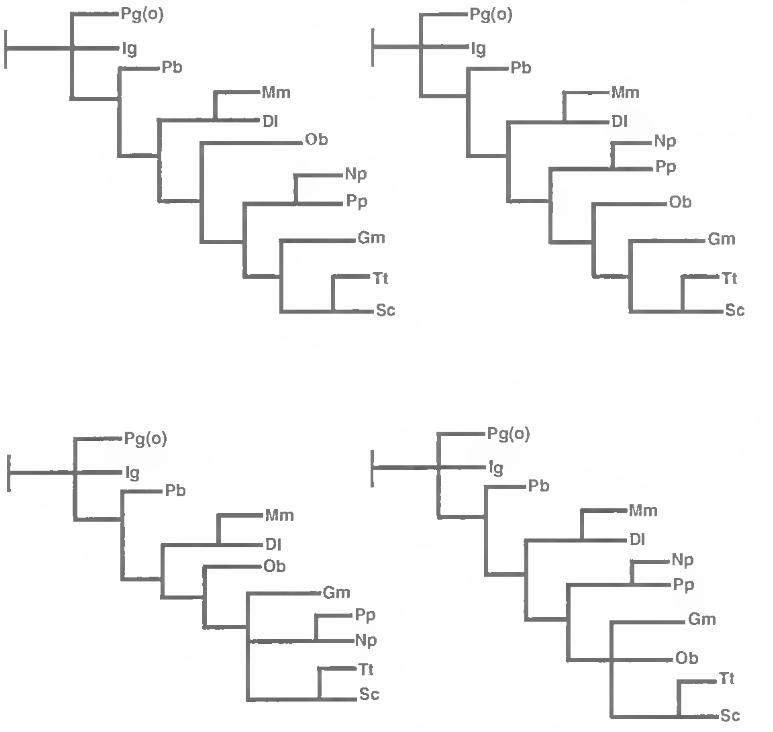

FIG. 40. Analysis 4; characters showing homoplasy or questionable polarity masked. Cladogram length 33; consistency index 69; retention index 68.

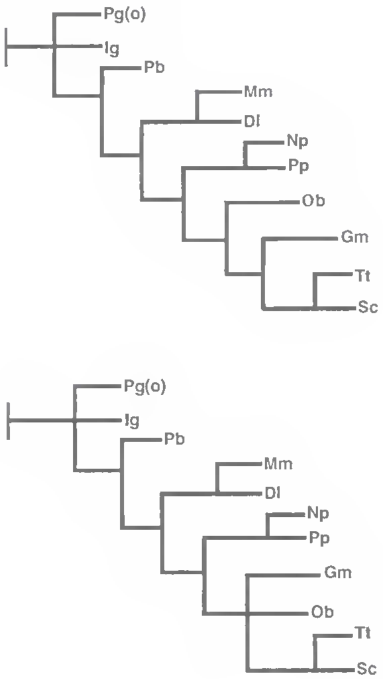

FIG. 41. As in Analysis 4, but with attachment to mastoid pad masked. Cladogram length 31; consistency index 70; retention index 67.

shape of anterior process of periotic) were masked.

In all 4 cladograms produced (Fig. 40A-D), *Monodon* and *Delphinapterus* were separated from *Phocoena, Neophocaena, Orcaella* and the delphinid genera. However, in two cladograms (Fig. 40A,B) *Orcaella* was separated from *Phocoena, Neophocaena* and all the delphinids. Analysis of the ancestral states suggested that this is based on the ventral attachment of the tympanoperiotic bones to the mastoid pad of the zygomatic arch. This was confirmed by re-running the analysis with that character masked (Fig. 41A,B) producing two cladograms identical to Fig. 40C,D.

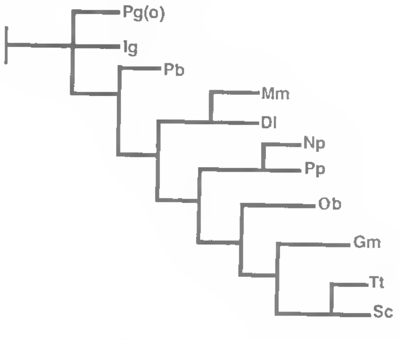

FIG. 42. As in Analysis 4, but with all characters of tympanoperiotic bones retained, despite equivocal polarity. Cladogram length 42; consistency index 69, retention index 71.

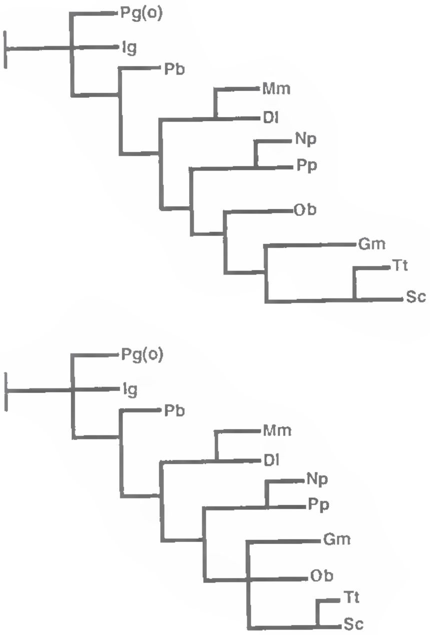

FIG. 43. Analysis 6; characters showing homoplasy and multistate attributes masked. Cladogram length 40; consistency index 75; retention index 78.

Because of the significance given to the tympanoperiotic bones, Analysis 5 retained tympanoperiotic characters, despite the equivocal polarity. The cladogram (Fig. 42) was identical to Figs 37B,38,40C,41A. Even with all tympanoperiotic characters retained, *Monodon* and *Delphinapterus* are linked, while *Orcaella* is linked with *Phocoena, Neophocoena* and the delphinids.

Coding continuously varying multistate characters (e.g. rostrum length, breadth of lower tympanic aperture) involves a more or less arbitrary decision on where to set the limits of the various categories. This introduces a bias so in Analysis 6 multistate characters were masked. Analysis with characters exhibiting homoplasy and multistate characters masked (i.e. comparable to Analysis 2) produced 2 trees (Fig. 43A,B) with *Monodon* and *Delphinapterus* as a sister group to

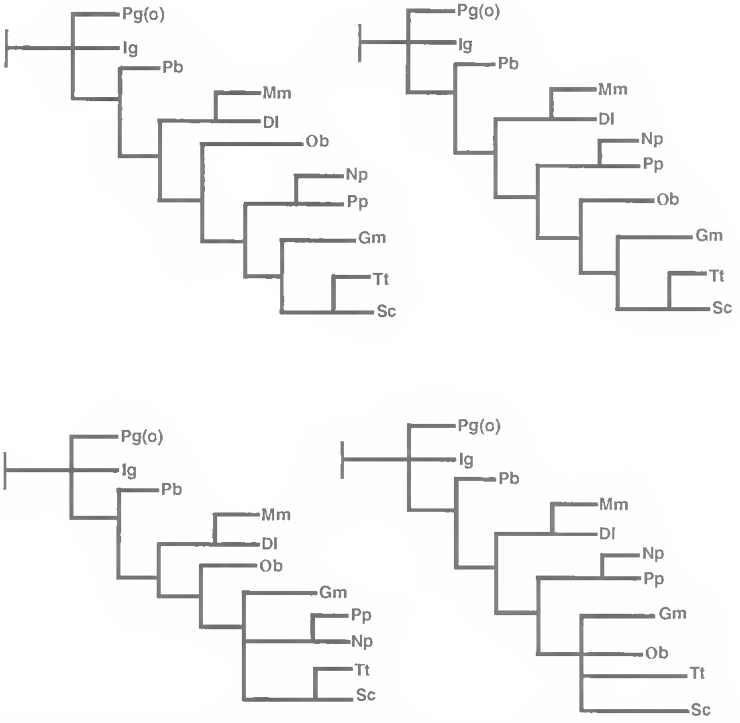

FIG. 44. Analysis 7; characters showing homoplasy or questionable polarity or multistate attributes masked. Cladogram length 30; consistency index 73; retention index 73.

Phocoena, Neophocaena, the delphinids and *Orcaella*. In both cases *Orcaella* was linked with the delphinids as the most derived taxa. This analysis, with a shorter length of 40 (due to fewer attributes), has the highest consistency index (0.75) and retention index (0.78) of all analyses.

In Analysis 7 any multistate characters not already deleted because of homoplasy or questionable polarity were masked. This is comparable to Analysis 4, and produced the same set of cladograms (Fig. 44A-D). The length was shorter (30 vs 33) because of the fewer characters but the consistency and retention indices were lower than in Analysis 6. A Nelson consensus tree was determined using option ‘nelsen’ of Hennig86 (Fig. 45).

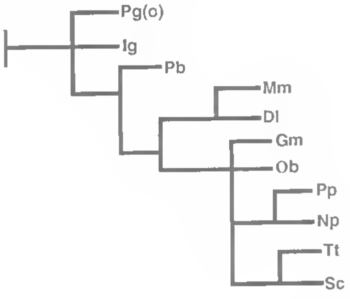

FIG. 45. Nelson consensus tree based on Analysis 7.

Analysis 7 and Analysis 4 were apparently driven by ventral attachment of the tympanoperiotic in *Orcaella*. Analysis 8 was the same as Analysis 7 except that attachment of the tympanoperiotic bones was also masked. The 2 cladograms (Fig. 46A,B), which were the same as Fig. 41A,B had consistency index (0.75) comparable to Analysis 6, but lower retention index (0.73). The Nelson consensus tree is Fig. 47.

DISCUSSION

TAXONOMIC RELATIONSHIPS OF MONODONTIDAE-PHOCOENIDAE-DELPHINIDAE. The cladograms consistently separated phocoenids and delphinids from the monodontids *Delphinapterus* and *Monodon*, and could even intersperse the phocoenids with the delphinids; this suggests that the phocoenids and

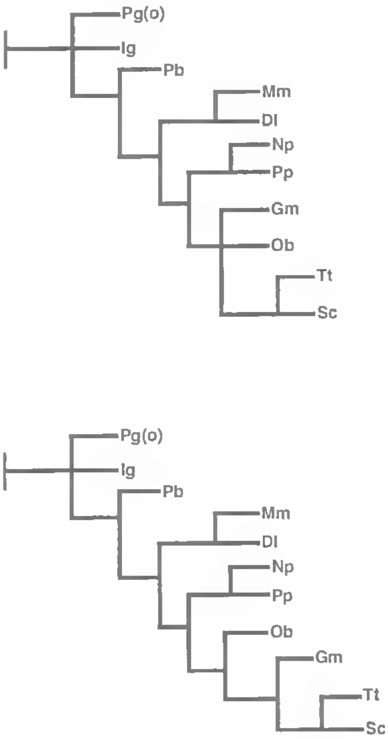

FIG. 46. Analysis 8; as in Analysis 7 but with ventral attachment of the tympanoperiotic bones masked. Cladogram length 28; consistency index 75; retention index 73.

delphinids together form the sister group to the monodontids. This extends previous studies (Heyning, 1989; Gretarsdottir & Arnason, 1992; Milinkovitch et al., 1994) in which the Monodontidae-Phocoenidae-Delphinidae remained an unresolved trichotomy.

We could not demonstrate any synapomorphies for the delphinid–phocoenid clade. Heyning (1989) indicated one, 'extreme reduction of zygomatic process of squamosal'. He considered the zygomatic process reduced in *Orcaella,* but we have shown that the zygomatic arch is substantial with a prominent mastoid section and that the mastoid pad provides the attachment point for the tympanoperiotic bones. On this character, *Orcaella* would be excluded from the phocoenid-delphinid clade. This occurred in our cladogram when 'attachment of the tympanoperiotic bones' was not masked. We suggest that form of the zygomatic arch is a reversal and not primitive in *Orcaella*; this is based on a series of synapomorphies it shares with the Delphinidae (Implications for previous classifications, below). Heyning (1989) characterized the zygomatic arch of the delphinid *Orcinus* as 'substantial', an implied reversal which he associated with the handling of large prey by killer whales. The poorly developed mesethmoid plate in *Orcaella* is possibly primitive, linking it more with phocoenids than delphinids. We suggest, however, that the poorly developed mesethmoid plate is a neotenic feature, most apparent in Australian material.

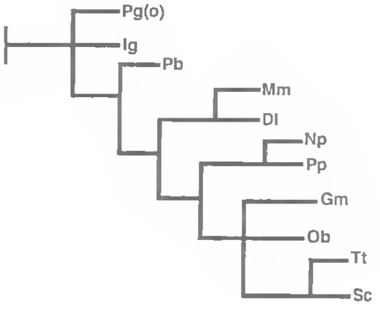

FIG. 47. Nelson consensus tree based on Analysis 8.

Monodontids and phocoenids have a suite of characters including short rostrum, no beak, short mandibular symphysis, poorly developed mesethmoid plate, widely separated pterygoid hamuli, and relatively unspecialized pre- and post-orbital lobes (especially so in monodontids). As our cladograms suggest that these families are the closest living relatives of delphinids, by outgroup comparison we would expect the features just listed to also occur in the most primitive of the delphinids. This suggests that blunt-headed *Pseudorca, Orcinus, Globicephala* and *Orcaella*, as well as *Cephalorhynchus* (which shows many parallels to phocoenids) are the most primitive delphinids. The alternative suggestion is that long-beaked delphinids such as *Sotalia* and *Sousa* are the most primitive extant delphinids (e.g. Kellogg, 1928; Fraser & Purves, 1962, using the Stenidae) and that the blunt-headed genera are convergent. Three lines of evidence can test the alternatives: (1) molecular data; (2) more extensive fossil material and (3) anatomical studies to determine whether the morphology of blunt-headed odontocetes is homologous. The molecular phylogeny of Milinkovitch et al. (1994, fig.1) is consistent with our cladograms, in that monodontids and phocoenids are separated from the delphinids as potential sister groups. To that extent their results support the possibility that blunt headed dolphins are primitive. Anatomical studies (Mead, 1975; herein) suggest, however, that the facial anatomy may be quite diverse and non-homologous in 'blunt-headed' dolphins. The anatomy of the facial region is generally considered to reflect adaptations to sound production (Heyning, 1989; Heyning & Mead, 1990) and features of the skull may reflect such modifications. Thus the possibilities of convergence are extensive. The demonstration of neotenic features of the skull in *Orcaella* provides a mechanism whereby more generalized features may be expressed, without implying that the taxon is primitive. The polarity of each character used in classification will therefore have to be examined before the alternative interpretations can be properly evaluated.

IMPLICATIONS FOR PREVIOUS CLASSIFICATIONS. Despite differences between our various analyses, the following were consistent: 1, *Monodon* and *Delphinapterus* were linked; 2, *Orcaella* was not linked with *Delphinapterus* (3) *Phocoena* and *Neophocaena* were linked; 4, *Phocoena, Neophocaena, Orcaella* and the delphinids were the sister group to *Monodon* and *Delphinapterus*; and 5, *Tursiops* and *Sousa* were linked, as the most derived branch.

Fourteen characters were not used (Appendix 2), usually because of insufficient comparative data. Available information for these characters is consistent with the results just outlined, except for the immunological and electrophoretic data of Lint et al. (1990) which is discussed later. The linking of *Tursiops* and *Sousa* may reflect the limited subset of delphinids used and is the most weakly supported of our conclusions. The other results have more general implications for the classifications in Fig. 1:

1. OWEN (1866) (Fig. 1A). *Orcaella* is never linked with *Phocoena* and *Neophocaena* in our cladograms. When Owen described *O. brevirostris*, the concept of *Phocoena* was broader than it is today. *Orcaella* has a dorsal extension of the pre-orbital lobe, as in phocoenids. However, this extension was intermediate in development between that in phocoenids and that shown by delphinids such as *Pseudorca* (pers. obs). *Orcaella* has none of the other synapomorphies of phocoenids (e.g., premaxillary boss, spatulate teeth, folded vestibular sacs).

2. KASUYA (1973) (Fig. 1B). *Monodon* and *Delphinapterus* were consistently linked, even when all tympanoperiotic bone characters were included (Fig.41). Our results do not support their family level separation (Kasuya, 1973); they validate Gray's (1821) Monodontidae. This family is as diagnosed by Tomilin (1967, as Delphinapterinae) and Rice (1984), except that the periotic bones do not appear to be fused to the squamosal as stated by the former author. The fossil *Denebola* Barnes, 1984 would also be included in the family, based on the anterior position of its orbits and the extensive border of the nares by the maxillary bones. Other fossils presumed to be monodontids (e.g. in Pilleri et al. 1989) need to be re-evaluated.

Orcaella and the delphinids were linked in our cladograms based on the absence of a posterior nasal sac and the lateral orientation of the posterior process of the tympanic bulla. We have shown elsewhere that characters of the tympano-periotic bones proposed as the basis for the Delphinapteridae by Kasuya (1973) and Pilleri et. al. (1989) are variable or provide only equivocal support. Moreover, *Orcaella* shared none of the synapomorphies identified for *Delphinapterus* (anterolateral margins of superior nares bordered by maxillaries, curvature of flippers & convex profile of skull), nor the undivided cranial sinuses, retention of lateral and superior lamina of the pterygoid bones & anterior position of the orbits with associated prominent palatine bridge under the orbit. Hence we found no support for the Delphinapteridae Kasuya, 1973. Other features used to unite *Orcaella* with *Delphinapterus* appear to be either primitive characters or have proved to be variable when a larger series of specimens were examined. In the first category is the flexibility of the head and cervical sinus, shared not only with beluga but also with river dolphins, such as *Inia*, and *Neophocaena*. Despite statements to the contrary, this flexibility is not associated with separate cervical vertebrae: while these are separate in monodontids and river dolphins, *Orcaella* has the atlas and axis fused as in most delphinids.

The light colour may be a feature of riverine populations, but the Queensland animals at least have a three-tone colour pattern such as in *Tursiops*, rather than the more diffuse pattern of monodontids. The lack of a beak and abbreviate melon are primitive features shared not only with beluga but also phocoenids such as *Neophocaena*. Moreover, the melon in *Orcaella* appears distinct from that in beluga. Similarities in general appearance led Mitchell (1975) to suggest 'a phyletic relationship' between *Orcaella* and 'the Arctic white whale', but we believe that the features are either shared primitive characters or convergent. We similarly suggest that ventral attachment of the tympanoperiotics in *Orcaella* is a primitive feature shared with monodontids and river dolphins such as *Platanista*, and thus has no taxonomic significance .

Characters which are more variable than originally described include most of the features of the tympanoperiotic bones, such as the posterior orientation of the posterior process of the bulla, width of posterior branch of lower tympanic aperture and the supposedly diagnostic statistics of the periotic triangle. The orientation of the processes and width of the LTA also characterize phocoenids, as much as *Delphinapterus*. Our larger series of specimens indicates that an olecranon process is usually present in *Orcaella* (Fig. 48A,B; cf. de Muizon, 1988), as in many delphinids but not *Delphinapterus* or *Monodon* which lack an olecranon process (Tomilin, 1967). The deltoid tuberosity of the humerus is more extended in *Orcaella* than in most delphinids (associated with the greater length of the humerus) but is not as subdistal as in monodontids (de Muizon, 1988, fig. 22). It, therefore, provides only equivocal evidence that *Orcaella* is a monodontid (cf. de Muizon, 1988).

Phocoena and *Neophocaena* were consistently linked most closely with *Orcaella* and delphinids *Tursiops*, *Sousa* and *Globicephala*; this does not support wide separation of the Phocoenidae and Delphinidae as in Fig. 1B.

3. BARNES (1984), GASKIN (1982)(Fig. 1C). Both authors linked the phocoenids and delphinids as in our cladograms. However, their linking *Monodon*, *Delphinapterus* and *Orcaella* in the same family contrasts with our findings. Including *Monodon* and *Delphinapterus* in the same family implicitly rejects the orientation of the posterior processes of the bulla and periotic, the compression of the bulla and the width of the lower tympanic aperture as valid family characters, since these all differ in the two genera. However, orientation of the posterior processes and width of the tympanic aperture were the two main characters used to unite *Orcaella* and *Delphinapterus* in the Delphinapteridae.

As discussed above, other characters which link these genera are shared primitive features, most of which could be equally used to support a relationship between *Orcaella* and the phocoenids.

Miller (1923) placed *Delphinapterus* and *Monodon* in different subfamilies based on differences in dentition, the pterygoid hamuli and extent to which the alisphenoid was overspread by the superior lamina of the pterygoids. Except for dentition, these features are not known for *Denebola*, the only other monodontid accepted in this paper. Although *Monodon* and *Delphinapterus* are distinct, we question the need for subfamily separation.

4. PILLERI et al. (1989) (Fig. 1D). This classification suffers from the same inconsistencies noted in the last section. In addition, the phocoenids and delphinids were widely separated, the former being placed with the river dolphins *Platanista, Inia* and *Pontoporia*. None of our cladograms support this classification: phocoenids differ from the river dolphins in profile of the tympanic bulla, shape of the sigmoid process, loss of lateral furrow, symmetry of vestibular sacs, roofing of the temporal region, position of the orbits relative to nares and complexity of the cranial sinuses. We consider the delphinids and phocoenids closely related based on morphology (de Muizon, 1988, 1990; Heyning, 1989), and ribosomal DNA (Milinkovitch et al., 1993). This relationship is also consistent with the molecular phylogeny in Milinkovitch et al. (1994), which included the river dolphin *Inia*.

5. LINT et al. (1990) (Fig. 1E). Our results agree with placing *Orcaella* in the Delphinidae. The major discrepancy in their classification is the extreme separation of phocoenids and delphinids. As indicated in the previous section, this is not supported by any of our cladograms and is inconsistent with most previous classifications. It was based on a combination of immunological and electrophoretic results, the latter incorporating the data of Shimura & Numachi (1987). Shimura & Numachi (1987) used a limited range of species; the ziphiid *Berardius* was the only non-delphinid taxon compared with phocoenids. It is thus possible that ziphiids and phocoenids were linked in the phenogram because they both differed from delphinids, rather than because they were closely related. Even with the extra species considered by Lint et al. (1990), the analysis was biased heavily towards delphinids, which may affect their conclusions on relationships among higher odontocete taxa.

6. FRASER & PURVES (1962) (Fig. 1F). We place *Orcaella* in the Delphinidae, as proposed by Fraser & Purves (1962). There are two aspects of their classification which we would question. The first is the linking of *Sousa, Sotalia* and *Steno* in the Stenidae, which is considered a more primitive taxon than the Phocoenidae. Grouping *Steno, Sotalia* and *Sousa* as the Stenidae (Fraser & Purves, 1962) is based on inconsistent or unclear criteria. The rugose teeth of *Steno*, proposed as a primitive character, is not shared by the other two

genera. The elongate rostrum and elongate mandibular symphysis, appear to be variable features in other odontocete families (Heyning, 1989) and may not be primitive. The length of rostrum appears to be particularly subject to reversals and convergences: a long rostrum occurs not only in less derived taxa such as *Platanista* but in more specialized taxa, such as *Stenella*, which we consider among the most derived of delphinids. Previous authors (Kellogg, 1928) emphasized the resemblance of kentriodontids and long-snouted dolphins such as *Sotalia* (closely related to *Sousa*). In light of the much more primitive form of the kentriodontid skull (e.g. lacking asymmetry), the resemblance may be superficial and dependent on variable features such as rostrum length and length of mandibular symphysis. Fraser & Purves (1962) pointed out the mixture of supposedly primitive characters and an advanced cranial sinus system in *Sotalia* and *Sousa*. We have not examined *Sotalia* but our *Sousa chinensis* skulls suggest close coalescence of pre- and post-orbital lobes to surround the optic nerve, as inferred by Fraser & Purves (1962). In addition, the excavation of the bones in the sphenoidal region of *Sousa* skulls we examined was complex and similar to that in more advanced delphinids such as *Tursiops* and *Stenella*. The consistent grouping of *Tursiops* and *Sousa* as the most derived group in our cladograms further suggests a more derived condition for *Sousa* than recognized in the systems of Kellogg(1928) and Fraser & Purves (1962). We have to recognise the limited range of delphinids considered in our analysis, however, so that our results may be biased.

In most of our cladograms, the phocoenids appeared as less derived than the delphinids. In Figs 40B & 44B the phocoenids were aligned to *Tursiops* and *Sousa*, but the cladogram was unresolved. The more generalized state of phocoenids is further supported by studies of base pair length of repetitive DNA: the phocoenids shared the 1750 base pair length with other taxa such as ziphiids, monodontids, etc whereas the delphinids had a unique base pair length of around 1580. The phocoenids were separated, with monodontids, from the delphinids in the molecular phylogeny of Milinkovitch et al. (1994). The phocoenids, nonetheless, show specializations (e.g. dorsal extensions of the preorbital pterygoid lobe, morphology of the nasal region which was considered by Klima & van Bree (1985) to be more derived in *Phocoena* than in other odontocetes examined). These specializations may reflect a long period of separation from the delphinids. The large number of synapomorphies for the Phocoenidae suggests it is a conservative body plan, although many of the characters are variably expressed throughout the family (Perrin pers. comm.; Appendix 2). Our results do not support the classification (Fraser & Purves, 1962) which placed the Phocoenidae between the Stenidae (including *Sousa*) and the Delphinidae.

An even greater disparity occurs between our results and the position of the Monodontidae in Fraser & Purves' (1962) classification. They considered the undivided form of the pterygoid sinuses a primary feature and the basis for their Superfamily Monodontoidea. As argued elsewhere, this feature needs to be confirmed by dissection. Beluga and narwhal appear to be more primitive than *Phocoena*, *Neophocaena* and delphinids (Figs 37–47). However, Fraser & Purves (1962) suggested that they are more primitive than all odontocetes other than ziphiids.

Monodon and *Delphinapterus* are consistently linked with *Phocoena*, *Neophocaena* and delphinids (Figs 37–47) arguing for their retention within a single taxon, such as the Delphinoidea (Heyning, 1989). Moreover, characters linking monodontids with *Phocoena*, *Neophocaena* and delphinids are derived features whereas those linking them to river dolphins are primitive or of questionable polarity (e.g. anterior position of orbits). Although Heyning (1989) and de Muizon (1988) did not resolve relationships between monodontids, delphinids and phocoenids, their analyses showed they form the most derived group of living odontocete taxa. Grouping monodontids, phocoenids and delphinids is also supported by some chemical data, such as the distribution of isovaleric acid in acoustic fat (Litchfield et al., 1975; Appendix 2). This grouping was also evident in molecular phylogenies (Milinkovitch et al., 1994). de Muizon (1988) and Heyning (1989) indicated a series of synapomorphies for physeterids and river dolphins (*Platanista, Inia, Pontoporia, Lipotes*), all of which would have to be considered reversals if Fraser & Purves' (1962) position of monodontids was accepted. Our results support de Muizon (1988, 1990) and Heyning (1989), indicating that the undivided pterygoid sinuses must be considered a reversal rather than a primary feature in monodontids. This removes the basis for separating beluga and narwhal in their own superfamily.

7. NISHIWAKI (1963, 1964, 1972) (Fig 1G). Nishiwaki (1963, 1964) proposed the Orcellidae

('Orcaelidae' of Nishiwaki 1972), with: 1, only atlas and axis fused; 2, size less than 12 feet (4 m); 3, no beak and less than 20 teeth in each row of the upper jaw. The first two characters are also consistent with the Delphinidae as defined by Nishiwaki. Although he characterized delphinids as having a distinct beak, he included genera such as *Cephalorhynchus* where the beak is reduced or absent. The only character separating *Orcaella* from delphinids is tooth number, but this seems a questionable basis for family separation given the variability in tooth number within other families (e.g. phocoenids). This character would no longer hold if *Grampus*, put in its own family by Nishiwaki, is considered a delphinid (Mead, 1975). Moreover, fossil *Tursiops* have as few as 14 teeth per side of each jaw (Barnes, 1990).

While we have reservations about the validity of the characters used by Nishiwaki, *Orcaella* does have characters (e.g. attachment of the tympanoperiotics to the mastoid pad of the zygomatic arch, the development of the zygomatic arch) which separate it from the delphinids and phocoenids. These characters could indicate a distinct family for *Orcaella*. We reject this option because *Orcaella* shares several derived features with the Delphinidae, including loss of posterior nasal sac, 1580 bp length of repetitive DNA, maintenance of the right premaxillary close to the nasals, apical position of nasals, development of the mesethmoid plate (de Muizon, 1988; Heyning, 1989; Barnes, 1990; Gretarsdottir & Arnason, 1992), although the last feature may vary between populations. These features imply a commonality of the most recent ancestor. Although some of the cladograms (e.g. Fig. 37B) indicate a basal position among delphinids for *Orcaella*, none suggested that it is a distinct family. The most parsimonious conclusion is that the zygomatic arch and attachment of the tympanoperiotic bones in *Orcaella* are reversals. The other characters which separate *Orcaella* from delphinids are either unique to *Orcaella*, or probably neotenous; in either of these cases they are of no value in assessing relationships between taxa. To emphasize them, rather than evidence for most recent common ancestor, promotes a system based on discordancy, characterised by an ever increasing number of monotypic taxa.

8. SLIJPER (1936), FORDYCE (1984), DE MUIZON (1988), HEYNING (1989), etc. (Fig. 1H). We agree with the 'classic' placement of *Orcaella* in the Delphinidae s.l. *Orcaella* was commonly (Figs 40c, 41a, 43a, 46b) placed as the least derived in the series *Orcaella*, *Globicephala* and (*Tursiops* + *Sousa*). However, equally commonly (Figs 40d, 41b, 43b, 46a) there was an unresolved trichotomy of *Orcaella*, *Globicephala* and (*Tursiops* + *Sousa*). Gray (1866, 1871), Anderson (1879), Fraser & Purves (1962), Mead (1975), de Muizon (1988) and Heyning (1989) placed *Orcaella* with the 'blunt-headed' dolphins such as *Orcinus*, *Pseudorca* and *Globicephala*. We have indicated skull features (separation of the medial and lateral lobes of the palatines, posterior extension of the lateral lobe of the palatine bone) which link *Orcaella* with the 'blunt-headed' dolphins, especially *Globicephala* and *Pseudorca*. What is unresolved is whether these features are evidence of relationship or whether they are convergent, reflecting shared constraints on morphology (e.g., short rostrum). Fraser & Purves (1962) suggested a series of increasing specialization from *Pseudorca* to *Orcinus*, *Orcaella*, *Globicephala* and *Feresa*. This was based on what we consider minor variations in the relative development of the pre- and post-orbital lobes, which have been largely inferred from skulls and not confirmed by dissection. In addition there can be considerable variation in the sinuses within taxa, e.g. *Pseudorca* (Fraser & Purves, 1962; Purves & Pilleri, 1978, fig. 18). *Pseudorca* was apparently placed as most primitive because of the more extensive development of the bony lateral lamina of the sinuses. However, this is formed from the palatine bone, rather than the lateral lobe of the pterygoid bone, as in monodontids and some river dolphins which were considered less derived by Fraser & Purves (1962). The lamina may not be homologous among these genera.

de Muizon (1988) placed *Orcaella* in the Globicephaliinae based on 'dilation of the premaxillae at apex of rostrum'. He illustrated the tip of the snout of *Orcaella*, composed entirely of premaxillae. However, the maxillae do not reach the tip in delphinids such as *Tursiops* or *Sousa* (pers. obs). Moreover, neither the premaxillae nor the rostrum show the broad transverse expansion as in *Pseudorca*, and especially *Globicephala melas*. Premaxillae/rostrum width at 0.75 length in *Orcaella* was 65.0% (56.0%–73.1%), which is comparable to *Lagenorhynchus* (Sergeant & Fisher, 1957) or *Tursiops* (Ross, 1977) in the Delphiniinae *sensu* de Muizon.

Cladograms, which place phocoenids and monodontids as the nearest living relatives of delphinids, suggest by outgroup analysis that features such as short rostrum of skull, widely separated pterygoid hamuli and unspecialized cranial sinuses are primitive within the delphinids. Similarities of *Orcaella* to phocoenids, especially *Neophocaena*, as well as monodontids, suggests it is one of the most primitive of the delphinids. Dudok van Heel (in Kamminga et al., 1983) suggested that *Orcaella* was one of the 'oldest "modern" species.."forced" inshore by more recent newcomers'. Although we have reservations about invoking competition to explain delphinid distributions, our data are consistent with *Orcaella* being a less derived taxon (at least within the Delphinidae, *s.l.*). Such an interpretation reinforces the generalized nature of genera such as *Cephalorhynchus* (which shows many parallels to phocoenids), as well as *Pseudorca*, *Orcinus* and *Orcaella*. The generalized features in these genera make it difficult to establish natural groupings of such genera based on shared derived features. Moreover, Mead (1975) indicated the wide morphological diversity in the facial anatomy of 'blunt-headed' dolphins which suggests that they may not be a natural group. *Grampus* and *Peponocephala*, in particular, fit poorly with the other genera at least based on the cranial sinus anatomy. Given the generalized and apparently primitive characters which link them, it is difficult to assess whether *Pseudorca, Orcinus* and *Globicephala* form a natural grouping, and whether *Orcaella* is related to any of them. *Orcaella*, for instance, has relatively few teeth, but they are not enlarged as in the other genera (e.g. *Pseudorca*, which has enlarged teeth even in the foetus: Pilleri & Purves, 1978, fig. 17).

Cladistic analyses assume that convergence is not so widespread that it masks underlying phylogenetic patterns; by outgroup analysis features of *Orcaella* are assumed to be primitive. The evidence for convergence in toothed whales is overwhelming, however, for characters such as rostrum length and probably mandibular symphysis length. A lack of knowledge of the functional significance of many of the other features used in cetacean classification (e.g. facial anatomy) prevents a balanced consideration of the extent of convergence in delphinids and other odontocetes. Neoteny in *Orcaella* further complicates interpretation; it provides a mechanism whereby apparently primitive features could occur in a more derived species. We conclude that *Orcaella* is not a monodontid or delphinapterid (sensu Kasuya, 1973). The balance of evidence suggests it is a delphinid *s. l.* However, given the ambiguity of characters used to define groupings within the Delphinidae and limitations in the comparative material of delphinids available to us, we did not consider it worthwhile to pursue our cladistic analyses further (e.g. by using different combinations of delphinid genera) in order to place *Orcaella* within the family. Recent DNA studies may provide important new evidence on the relationships of toothed whales. However, rigorous phylogenetic techniques on a wider range of characters than were available for this study, should be rewarding. Such studies will also provide the necessary tests for taxonomic hypotheses generated by DNA and other molecular techniques.

ACKNOWLEDGEMENTS

We thank H. Marsh, B. Dowd, R. Kenchington, A. Spain, A. Birtles, M. Devereux, G. Hopper, E. Drom, L. Price, M. Downes, A. Witting, T. Heinsohn, R. Heinsohn, A. Haffenden, J. Lanyon, A. Preen, K. Saalfeld (all at James Cook University), T. McNamara (Queensland Dept. Primary Industries) & K.Adler (Queensland Dept Environment & Heritage) for help with carcass salvage. We thank J. Hoey (Great Barrier Reef Aquarium) for access to freezer space. We thank Bill Dowd for careful preparation of the skeleton of MM1015. Robert Patterson and Steve Van Dyck provided access to the Queensland Museum collection. For similar help, we would like to thank F. Scott (Nova Scotia Museum of Natural History, Halifax, Nova Scotia), D. Balkwill (Canadian Museum of Nature, Ottawa, Ontario), J. Ford and education staff at the Vancouver Aquarium (Vancouver, British Columbia), and D. Canning (Dept. of Zoology, University of British Columbia). A. Preen (James Cook University) provided a specimen of *Neophocaena* and made observations for us on live *Orcaella* at the Jaya Ancol Aquarium, Jakarta, Indonesia. We thank J.L. Bannister for examining *Orcaella* in the Western Australian Museum and R. Sabin for examining the holotype. Preparation of teeth and counting of dentinal growth rings were carried out by N. Goudberg, under the direction of Helene Marsh (James Cook University). A. Williamson helped measure tympanoperiotic bones. We also thank Helene Marsh for access to literature. We thank Bruce Cowell (Queensland Museum), R. Yeldham (James Cook University) and M. Pulsford (Natural History Museum) for photography and J. True (Museum of Tropical Queensland) for Fig. 1. We thank C. de Muizon (Institut Francais d'Etudes Andines, Lima, Peru) and B. Kamminga (Delft University of Technology, Delft, The Netherlands) for papers and comments on *Orcaella*. For helpful comments, we are grateful to D. Bellwood (James Cook University), D. Gaskin (University of Guelph), J. Mead (Smithsonian Institution), C. Wallace (Museum of Tropical Queensland), W.F. Perrin (Southwest Fisheries Science Centre, La Jolla, California) and G.J.B. Ross (Australian Biological Resources Study, Canberra).

LITERATURE CITED

ANDERSON, J. 1879. Anatomical and zoological researches comprising an account of the zoological results of the two expeditions to western Yunnan in 1868 and 1875; and a monograph of the two cetacean genera *Platanista* and *Orcella*. (B. Quaritch: London).

ARNOLD, P.W. & GASKIN, D.E. 1975. Lungworms (Metastrongyloidea: Pseudaliidae) of harbour porpoise *Phocoena phocoena* (L., 1758). Canadian Journal of Zoology 53: 713-735.

BARNES, L.G. 1984. Fossil odontocetes (Mammalia: Cetacea) of the Almejas Formation, Isla Cedros, Mexico. Paleobios 42: 1-46.

1985. Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). Marine Mammal Science 1: 149-165.

1990. The fossil record and evolutionary relationships of the genus *Tursiops*. pp. 3-26. In Leatherwood,S. & Reeves, R. The bottlenose dolphin. (Academic Press: Sydney).

COWLEY, L.F. 1944. The skull of the false killer whale *Pseudorca crassidens*. Proceedings of the Zoological Society of London 114: 328-387.

CURRY, B.E. 1992. Facial anatomy and potential function of the facial structures for sound production in the harbour porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*). Canadian Journal of Zoology 70: 2103-2114.

DAWBIN, W.H. 1972. Dolphins & whales. pp. 270-276. In Ryan, P. (ed.) Encyclopedia of Papua New Guinea. (Melbourne University Press: Melbourne).

DAWBIN, W.H., NOBLE, B.A. & FRASER, F.C. 1970. Observations on the Electra dolphin *Peponocephala electra*. Bulletin of the British Museum of Natural History (Zoology) 20: 175-201.

EALES, N.B. 1950. The skull of the foetal narwhal *Monodon monoceros* L. Philosophical Transactions of the Royal Society of London 235B: 1-33.

1953 . The manus of the narwhal *Monodon monoceros* L. Proceedings of the Zoological Society of London 124: 201-211.

EVANS, H.E. & CHRISTENSEN, G.C. 1979. Miller's anatomy of the dog. (W.B. Saunders Company: London).

FARRIS, J.S. 1988. Hennig86. Hennig 86 Reference version 1.5.

FORDYCE, E. 1984. Evolution and zoogeography of cetaceans in Australia. pp. 929-948. In Archer, M. & Clayton, G. (eds). Vertebrate zoogeography and evolution in Australasia (Hesperian Press: Marrickville).

FORDYCE, E. & BARNES, L.G. 1994. The evolutionary history of whales and dolphins. Annual Review of Earth & Planetary Science 22: 419-455.

FOREY, P.L., HUMPHRIES, C.J., KITCHING, I.J., SCOTLAND, R.W., SIEBERT, D.J. & WILLIAMS, D.M. 1992. Cladistics. A practical course in systematics (Clarendon Press: Oxford).

FRASER, F.C. 1950. Two skulls of *Globicephala macrorhynchus* (Gray) from Dakar. Atlantide Report 1: 49-60.

FRASER, F.C. & PURVES, P.E. 1962. Hearing in cetaceans. Evolution of the accesory air sacs and the structure and function of the outer and middle ear in recent cetaceans. Bulletin of the British Museum of Natural History (Zoology) 7: 1-140.

GASKIN, D.E. 1982. The ecology of whales and dolphins. (Heinemann Education Books Inc.: Melbourne)

GOULD, S.J. 1977. Ontogeny and phylogeny. (Harvard University Press: Cambridge, Massachusetts).

GRAY, J.E. 1866. Catalogue of the seals and whales in the British Museum, 2nd edition.(British Museum: London).

1871. Supplement to the catalogue of seals and whales in the British Museum. (British Museum: London).

GRETARSDOTTIR, S. & ARNASON, U. 1992. Evolution of the common cetacean repetitive DNA component and the systematic position of *Orcaella brevirostris*. Journal of Molecular Evolution 34: 201- 208.

HEINSOHN, G. 1979. Biology of small cetaceans in north Queensland waters. Unpublished report to Great Barrier Reef Marine Park Authority.

HERSHKOVITZ, P. 1966. Catalogue of living whales. Bulletin of the United States National Museum 246: 1-259.

HEYNING, J.E. 1989. Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant odontoctes. Natural History Museum of Los Angeles County Contributions in Science 405: 1-64.

HEYNING, J.E. & MEAD, J.G. 1990. Evolution of the nasal anatomy of cetaceans. pp. 67-79. In Thomas, J. & Kastelein, R. (eds). Sensory abilities of cetaceans. (Plenum Press: New York).

HOYT, E. 1984. The whale watcher's handbook. (Penguin Madison Press Ltd: Toronto).

HUBER, E. 1934. Anatomical notes on Pinnipedia and Cetacea. pp. 107-134. In Packard, E.L., Kellogg, R. & Huber, E. (eds). Marine mammals, contributions to paleontology. (Carnegie Institution: Washington).

JOHNSON, D.P. 1964. Mammals of the Arnhem Land expedition. pp. 427-515. In R.L. Specht (ed.). Records of the American-Australian scientific expedition to Arnhem Land. Zoology. (Melbourne University Press: Melbourne).

KAMMINGA, C., WIERSMA, H. & DUDOK VAN HEEL, W.H. 1983. Investigations on cetacean sonar VI. Sonar sounds from *Orcaella brevirostris* of the Mahakan River, East Kalimantan, Indonesia; first descriptions of acoustic behaviour. Aquatic Mammals 10: 83-95.

KASUYA, T. 1972. Some information on the growth of the Ganges dolphin with a comment on the Indus dolphin. Scientific Reports of the Whales Research Institute 24: 87-108.

1973. Systematic consideration of recent toothed whales based on the morphology of the tympanoperiotic bone. Scientific Reports of the Whales Research Institute 25: 1-103.

KELLOGG, R. 1928. The biology of whales - their adaptation to life in the water. Quarterly Review of Biology 3: 29-76, 174-208.

KLEINENBERG, S.E., YABLOKOV, A.V., BELKOVICH, B.M. & TARASEVICH, M.N. 1969. Beluga (*Delphinapterus leucas*): investigation of the species. Israel Program for Scientific Translation translation from Izdatel'stvo Nauka (1964). (IPST: Jerusalem).

KLIMA, M. & VANBREE, P.J.H. 1985. Additional nasal structures in the skull of *Phocoena phocoena* and the morphogenesis of the nasal region in the odontocetes (in German). Gegenbaurs morph Jahrbuch Leipzig 131: 131-178.

KURAMOCHI, T., ARAKI, J. & MACHIDA, M. 1990. Pseudaliid nematodes from Dall's porpoise *Phocoenoides dalli*. Bulletin of the National Science Museum, Tokyo, series A, 16: 97-103.

LAWRENCE, B. & SCHEVILL, W.E. 1956. The functional anatomy of the delphinid nose. Bulletin of the Museum of Comparative Zoology 114: 103-151.

LEATHERWOOD, S. & REEVES, R. 1983. The Sierra Club handbook of whales and dolphins. (Sierra Club Books: San Francisco).

LINT, D.W., CLAYTON, J.W., LILLIE, W.R. & POSTMA, L. 1990. Evolution and systematics of the beluga whale *Delphinapterus leucas*, and other odontocetes: a molecular approach. pp. 7-22. In Smith, T.G., St Aubin, D.J. & Geraci, J.R. (eds). Advances in research on the beluga whale *Delphinapterus leucas*. Canadian Bulletin of Fisheries and Aquatic Science 224.

LITCHFIELD, C., GREENBERG, A.J., CALDWELL, D.K., CALDWELL, M.C., SIPOS, J.C. & ACKMAN, R.G. 1975. Comparative lipid patterns in acoustical and nonacoustical fatty tissues of dolphins, porpoises and toothed whales. Comparative Biochemistry and Physiology 50B: 591-597.

LLOZE, R. 1982. On the presence of os wurmiens in the skull of the Irrawaddy dolphin *Orcaella brevirostris* (Gray, 1866) (Cetacea: Delphinidae) (in French). 107th Congress national de la Societe savantes, Brest; sciences 2: 127-138.

LLOZE, R. undated. Manuscript on *Orcaella brevirostris* (Gray, 1866). Translated by Sir R. Harrison.

LONNBERG, E. 1910. Remarks on the dentition of *Delphinapterus leucas*. Arkiv for Zoologi 7: 1-18.

MARSH, H., LLOZE, R., HEINSOHN, G. & KASUYA, T. 1989. Irrawaddy dolphin *Orcaella brevirostris* (Gray, 1866). pp. 101-118. In Harrison, R.J. & Ridgway, S. (eds). Handbook of marine mammals, vol. 4. (Academic Press: Sydney).

MARTIN, A.R. 1990. Whales and dolphins. (Salamander Books Ltd: London)

MEAD, J.G. 1975. Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia: Cetacea). Smithsonian Contributions to Zoology 207: iv + 72 pp.

MILINKOVITCH, M.C., ORTI, G. & MEYER, A. 1993. Revised phylogeny of whales suggested by mitochondrial DNA sequences. Nature 361: 346-348.

MILINKOVITCH, M.C., MEYER, A. & POWELL, J.R. 1994. Phylogeny of all major groups of cetaceans based on DNA sequences from three mitochondrial genes. Molecular Biology & Evolution 11: 939-948.

MILLER, G.S. Jr. 1923. The telescoping of the cetacean skull. Smithsonian Miscellaneous Collections 76: 1-55.

MINASIAN, S.M., BALCOMB, K. & FOSTER, L. 1987. The whales of Hawaii. (Marine Mammal Fund: San Francisco).

MITCHELL, E.D. 1970. Pigmentation pattern evolution in delphinid cetaceans. Canadian Journal of Zoology 48: 717-740.

1975. Porpoise, dolphin and small whale fisheries of the world. Status and problems. IUCN Monograph 3. (International Union for Conservation of Nature: Morges, Switzerland)

MOORE, J.C. 1968. Relationships among the living genera of beaked whales with classifications, diagnoses and keys. Fieldiana Zoology 53: 209-298.

MORRIS, R.J. 1985. The acoustic faculty of dolphins. pp. 369-399. In Harrison, R.J. & Bryden, M (eds). Research on dolphins. (Clarendon Press: Oxford)

MUIZON, C. de. 1988. The phylogenetic relationships of the Delphinida (Cetacea, Mammalia) (in French). Annales de Paleontologie (Vertebres-Invertebres) 74: 159-227.

1990. A new Ziphiidae (Cetacea) from the early Miocene of Washington state, U.S.A. and phylogenetic analysis of the major groups of odontocetes. Bulletin de Museum national d'histoire naturelle, Paris, 4th series, 12: 279-326.

1993. Walrus-like feeding adaptation in a new cetacean from the Pliocene of Peru. Nature 365: 745-748.

in press. Are the squalodonts related to the platanistoids? Proceedings of the San Diego Society of natural History.

NISHIWAKI, M. 1963. Taxonomical consideration on genera of Delphinidae. Scientific Reports of the Whales Research Institute 17: 93-103.

1964. Revision of the article "Taxonomical consideration on genera of Delphinidae" in No. 17. Scientific Reports of the Whales Research Institute 18: 171-172.

1972. Cetacea: general biology. pp. 6-136. In Ridgway, S. (ed). Mammals of the sea. (C.C. Thomas: Springfield, Illinois).

OELSCHLAGER, H.A. 1986. Comparative morphology and evolution of the otic region in toothed whales (Cetacea, Mammalia). The American Journal of Anatomy 177: 353-368.

1990. Evolutionary morphology and acoustics in the dolphin skull. pp. 137-162. In Thomas, J. & Kastelein, R. (eds). Sensory abilities of cetaceans. (Plenum Press: New York).

OWEN, R. 1866. On some Indian Cetacea collected by Walter Elliot, Esq. Transactions of the Zoological Society, London 6: 17-47.

PATERSON, R. 1986. A list of specimens of the order Cetacea in the Queensland Museum. Memoirs of the Queensland Museum 22: 309- 312.

1994. An annotated list of recent additions to the Cetacean collection in the Queensland Museum. Memoirs of the Queensland Museum 35: 217-223.

PERRIN, W.F. 1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. Bulletin of the Scripps Institution of Oceanography 21: 1-206.

PERRIN, W.F. & HUBBS, C. 1969. Observations on a young pygmy killer whale (*Feresa attenuata* Gray) from the eastern tropical Pacific ocean. Transactions of the San Diego Society of Natural History 15: 297-305.

PETTER, A.J. & PILLERI, G. 1982. *Pharurus asiaeorientalis* new species, metastrongylid nematode, parasite of *Neophocaena asiaeorientalis* (Phocoenidae, Cetacea). pp. 141-148. In Pilleri, G. (ed.) Investigations on Cetacea, vol. 13.

PILLERI, G. 1976. The black finless porpoise is not black. pp. 161-164. In Pilleri, G. (ed.). Investigations on Cetacea, vol. 7 .

1980. Sonar field patterns in cetaceans, feeding behaviour and the functional significance of the pterygoschisis. pp. 147-158. In Pilleri, G. (ed). Investigations on Cetacea, vol. 11.

PILLERI, G. & GIHR, M. 1973-74. Contributions to the knowledge of the cetaceans of southwest and monsoon Asia (Persian Gulf, Indus delta, Malabar, Andaman Sea & Gulf of Siam). pp. 95-153. In Pilleri, G. (ed) Investigations on Cetacea, vol. 5.

PILLERI, G., GIHR, M. & KRAUS, C. 1982a. Osteological considerations on the shape of the sonar field in the narwhal (*Monodon monoceros*). pp. 205-221. In Pilleri, G. (ed). Investigations on Cetacea, vol. 13.

1982b. Considerations on the sonar emission field of *Pontoporia blainvillei* with osteological remarks on the pterygoid region of cetaceans. pp. 223-242. In Pilleri, G. (ed). Investigations on Cetacea, vol. 13.

1989. The organ of hearing in Cetacea. 2. Paleobiological evolution. pp. 5-185. In Pilleri, G. (ed). Investigations on Cetacea, vol. 22.

PILLERI, G., GIHR, M., ZUGANOV, V.V. & KRAUS, C. 1982. Fenestration of the skull in some cetaceans. pp. 149-192. In Pilleri, G. (ed). Investigations on Cetacea, vol 14.

PILLERI, G., ZBINDEN, K. & KRAUS, C. 1980. Characteristics of the sonar systems of cetaceans with pterygoschisis. Directional properties of the sonar clicks of *Neophocaena phocaenoides* and *Phocoena phocoena* (Phocoenidae). pp. 152-188. In Pilleri, G. (ed). Investigations on Cetacea, vol 11.

PLATNICK, N.I., GRISWOLD, C.E. & CODDINGTON, J.A. 1991. On missing entries in cladistic analysis. Cladistics 7: 337-343.

PURVES, P. & PILLERI, G. 1973. Observations on the ear, nose, throat and eye of *Platanista indi*. pp. 13-57. In Pilleri, G. (ed). Investigations on Cetacea, vol 5.

PURVES, P & PILLERI, G. 1978. The functional anatomy and general biology of *Pseudorca crassidens* (Owen) with a review of the hydrodynamics and acoustics in Cetacea. pp. 67-230. In Pilleri, G. (ed). Investigations on Cetacea, vol 9.

1983. Echolocation in whales and dolphins (Academic Press: Sydney).

RAVEN, H.C. & GREGORY, W.K. 1933. The spermaceti organ and nasal passages of the sperm whale (*Physeter catodon*) and other odontocetes. American Museum of Natural History Novitates 677: 1-18.

REEVES, R.R. & TRACEY, S. 1980. *Monodon monoceros*. Mammalian species No. 127 (American Society of Mammalogists: Kansas).

REIDENBERG, J.S. & LAITMAN, J.T. 1982. Position of the larynx in odontocetes (toothed whales). The Anatomical Record 218: 98-106.

RICE, D.W. 1984. Cetaceans. pp. 447-490. In Anderson, S. & Knox Jones Jr, J. (eds). Orders and families of recent mammals of the world. (John Wiley and Sons: New York).

RIDE, W.L., SABROSKY, G.W., BERNARDI, G. & MELVILLE, R. 1985. International Code of Zoological Nomenclature, 3rd edition. (The Natural History Museum: London).

ROMMEL, S. 1990. Osteology of the bottlenose dolphin. pp. 29-49. In Leatherwood, S. & Reeves, R. (eds). The bottlenose dolphin. (Academic Press: Sydney).

ROSS, G.J.B. 1977. The taxonomy of bottlenosed dolphin *Tursiops* species in South African waters, with notes on their biology. Annals Cape Provincial Museums Natural History 11: 135-194.

SCHENKKAN, E.J. 1973. On the comparative anatomy and function of the nasal tract in odontocetes (Mammalia, Cetacea). Bijdragen tot de Dierkunde 43: 127-159.

SERGEANT, D.E. & FISHER, H.D. 1957. The smaller Cetacea of eastern Canadian waters. Journal of the Fisheries Research Board of Canada 14: 83-115.

SHIMURA, E. & NUMACHI, K. 1987. Genetic variability and differentiation in the toothed whales. Scientific Reports of the Whales Research Institute 38: 141-163.

SLIJPER, E.J. 1936. Die Cetaceen, vergleichend anatomisch und systematisch, Diss Utrecht, 1936. Capita Zoologica 7(1).

1962. Whales. (Hutchinson & Co. Ltd: Sydney).

DE SMET, W.M.A. 1977. The regions of the cetacean vertebral column. pp. 59-80. In Harrison, R. (ed). Functional anatomy of marine mammals, vol. 3. (Academic Press: New York).

STEWART, B.E. & STEWART, R.E. 1989. *Delphinapterus leucas*. Mammalian Species No. 336. (American Society of Mammalogists: Kansas).

SYLVESTRE, J.-P. 1993. Dolphins & porpoises. A worldwide guide. (Strelin Publishing Company: New York).

TALBOT, F. & STEENE, R. 1984. Reader's Digest Book of the Great Barrier Reef. (Reader's Digest: Sydney).

TAS'AN, IRWANDRY, A., SUMITRO, D. & hENDROKUSUMO, S. 1980. *Orcaella brevirostris* (Gray, 1866) from Mahakam River. (Jaya Ancol Aquarium: Jakarta).

TAS'AN & LEATHERWOOD, S. 1984. Cetaceans live-captured for Jaya Ancol Oceanarium, Djakarta, 1974-1982. Report of the International Whaling Commission 34: 485-489.

TOMILIN, A.G. 1967. Cetacea. Mammals of the USSR and adjacent countries, vol. 9 (English translation from Akademia Nauka SSSR, 1957). (Israel Program for Scientintific Translaslation: Jerusalem).

TRUE, F.W. 1889. A review of the family Delphinidae. Bulletin of the United States National Museum 36: 1-189.

1910. An account of the beaked whales of the family Ziphiidae in the collection of the United States National Museum, with remarks on some specimens in other American museums. Bulletin of the United States National Museum 73: 1-89.

1912. Description of a new fossil porpoise of the genus *Delphinodon* from the Miocene formation of Maryland. Journal of the Academy of Natural Sciences of Philadelphia, 2nd series 15: 165-194.

VAN BENEDEN, P.J. & GERVAIS, F.L.P. 1868-1879. Osteography of the living and fossil Cetacea, consisting of the description and illustration of the skeleton and dentition of these animals (in French). (Libraire de la Societe Geographie: Paris).

VLADYKOV, V.D. 1943. A modification of the pectoral fin in the beluga from the St Lawrence River. Le naturaliste canadien 70: 23-40.

1944. Fishery, biology and economic importance of the "marsouin blanc" or beluga (*Delphinapterus leucas*) in the St Lawrence River and Gulf of St Lawrence (in French). (Quebec Dept Fisheries: Quebec city).

WATSON, L. 1985. Whales of the world. (Century Hutchinson Ltd: Hawthorn, Melbourne).

WINGE, H. 1921. A review of the interrelationships of the Cetacea. Smithsonian Miscellaneous Collections 72: 1-97.

APPENDIX 1: Measurements of tympano-periotic bones (after Kasuya, 1973). Measurements 1 and 13 in mm. Measurements 2-10 as % of standard length of tympanic bulla. Measurements 14-19, 23-28 as % of standard length of periotic.

TYMPANIC BULLA

1. Standard length of tympanic bulla, distance from anterior tip to posterior end of outer posterior prominence
2. Distance from anterior tip to posterior end of inner posterior prominence
3. Distance from posteroventral tip of outer posterior prominence to tip of sigmoid process
4. Distance from postero-ventral tip of outer posterior prominence to tip of conical process
5. Width of tympanic bulla at level of the sigmoid process
6. Height of tympanic bulla, from tip of sigmoid process to ventral keel
7. Width across inner and outer posterior prominences
8. Greatest depth of interprominential notch
9. Width of upper border of sigmoid process
10. Width of posterior branch of lower tympanic aperture

PERIOTIC

13. Standard length of periotic, from tip of anterior process to posterior end of posterior process, measured on a straight line parallel with cerebral border
14. Thickness of superior process at the level of upper tympanic aperture
15. Width of periotic across cochlear portion and superior process, at the level of upper tympanic aperture
16. Least distance between the margins of the fundus of internal auditory meatus and of aperture of ductus endolymphaticus (aquaeductus vestibuli)
17. Least distance between the margins of the fundus of internal auditory meatus and aperture of aquaeductus cochleae
18. Length of articular facet of the posterior process of periotic for the posterior process of tympanic bulla
19. Anteroposterior diameter of cochlear portion
22. Length of periotic shown by the percentage of length of tympanic bulla
23. Separation of foramen singulare and aquaeductus Fallopi
24. Angle of lateral margin of posterior process of tympanic bulla to sagittal axis

	JM 4700		JM 4705		JM 4709		JM 4712		JM 4720	JM 4721		JM 4725		JM 4726		JM 4734		JM 4735		JM11343	
	L	R	L	R	L	R	L	R	R	L	R	L	R	L	R	L	R	L	R	L	R
1*	34.95	34.80	36.00	36.15	36.25	36.50	33.50	33.70	33.70	35.00	33.85	35.20	35.60	35.20	34.90	34.20	34.35	35.30	35.20	33.05	33.75
2	96.42	99.71	95.56	95.16	95.17	93.15	93.73	96.14	94.66	93.57	94.98	96.73	95.79	92.90	97.28	94.74	97.96	94.33	94.60	96.97	94.37
3	60.37	58.33	63.75	59.06	62.20	62.74	64.18	64.54	63.65	63.14	65.29	59.38	58.57	62.07	61.6	60.53	64.05	58.07	58.52	66.26	65.93
4	43.20	42.67	44.86	44.54	44.83	44.11	47.01	47.03	45.70	42.71	45.79	39.77	41.29	42.33	41.98	42.84	45.85	40.65	41.19	47.20	47.41
5	57.08	57.04	55.83	53.94	57.93	58.08	59.85	60.98	58.01	56.71	58.05	57.24	54.63	59.66	60.03	58.77	57.50	58.07	58.66	57.03	58.67
6	79.11	77.87	75.56	74.69	71.31	69.86	77.01	76.85	77.74	76.14	77.1	72.73	72.61	77.13	77.22	76.32	78.02	72.52	74.57	72.62	72.30
7	62.37	61.35	58.19	53.94	57.52	56.30	61.49	62.01	58.75	57.86	58.94	56.96	55.62	62.35	62.61	60.09	60.55	57.50	58.24	56.58	55.70
8	36.19	34.63	28.19	31.54	27.86	32.6	30.14	29.97	33.53	30.86	32.34	28.69	33.14	31.39	33.95	27.92	28.23	25.78	25.99	29.65	22.52
9	33.05	33.62	20.42	19.36	-	-	-	-	-	20.14	17.28	-	-	22.44	-	20.03	18.78	20.82	19.89	22.09	-
10	5.72	6.75	5.28	6.92	7.45	6.30	6.27	6.97	7.42	5.86	6.2	6.53	6.18	5.68	6.02	6.29	6.4	5.67	7.24	7.26	8.89
13*	37.40	38.20	36.20	36.25	36.90	37.20	35.50	35.70	34.50	38.00	36.90	37.85	37.25	35.10	33.65	35.25	35.15	35.80	33.55	32.1	31.00
14	38.10	34.95	36.74	41.38	34.82	34.41	37.61	34.73	35.51	34.21	32.25	31.97	32.48	37.04	37.30	34.47	35.85	36.03	36.66	33.96	36.07
15	52.54	49.48	56.49	53.24	61.25	54.84	54.08	49.30	49.57	51.84	56.23	52.05	49.93	54.27	57.36	57.87	57.18	55.45	58.42	62.31	64.09
16	7.89	6.41	1.38	6.07	4.34	3.90	6.67	2.52	-	6.45	4.34	5.94	5.1	3.13	3.27	3.26	3.97	7.54	4.62	7.48	9.18
17	6.28	6.54	4.42	4.55	5.69	4.84	5.63	6.16	9.86	4.21	7.72	4.76	5.36	3.56	6.24	5.53	5.69	5.17	6.86	4.67	7.73
18	28.21	27.75	28.18	35.03	-	-	-	-	-	-	-	-	-	-	-	36.31	35.42	37.99	36.07	35.98	-
19	40.11	39.53	45.16	46.62	44.58	42.34	41.13	41.32	42.17	38.95	41.96	39.36	39.73	44.44	44.58	42.98	43.95	42.88	42.03	45.95	46.38
22	107.01	112.02	100.56	100.28	101.79	101.92	105.97	105.93	102.37	108.57	109.01	107.52	104.63	99.71	96.41	103.07	102.32	101.41	95.31	97.12	92.00
23										9.08	16.8	12.68	13.69	15.95	19.01	13.05	11.95	13.83	13.71	15.11	14.49
24	43°	39°	40°	35°	42°	28.5°	47°	34°	25°	33°	17°	43°	43°	32°	41°	40°	27°	33°	19°	47.5°	23.8°
25	25.67	26.57	30.39	27.86	25.20	22.04	25.35	24.93	28.26	26.58	25.54	28.00	27.79	29.63	32.39	33.19	32.57	30.87	28.17	34.42	38.33
26	3.74	4.97	6.22	5.79	-	-	-	-	-	-	-	-	-	-	-	5.53	4.55	6.56	7.00	5.61	-
27	10.29	7.85	7.73	8.69	7.86	9.27	8.17	9.29	7.54	7.89	9.49	8.72	9.13	8.97	9.96	8.37	8.39	9.36	9.99	10.12	-
28	10.29	-	12.02	10.07	-	-	-	-	-	-	-	-	-	-	-	11.49	8.53	11.31	10.73	11.68	11.59

25. Maximum width of fundus of the internal auditory meatus
26. Width of foramen ovale
27. Width of foramen rotundum
28. Width of head of malleus

APPENDIX 2: CHARACTER STATES

1. Vestibular sacs. Heyning (1989) demonstrated that vestibular sacs are a feature of all odontocetes except Physeteridae (including *Kogia*), Ziphiidae and *Platanista*. Schenkkan (1973) described vestibular sacs in ziphiids, but we follow the interpretation by Heyning, who had access to a wider range of material and used supplementary criteria such as position of the sacs relative to muscle layers. Lack of vestibular sacs is primitive by outgroup analysis, as suggested by Heyning (1989).

2. Folded vestibular sacs. This is a specialized feature of the Phocoenidae, as demonstrated by numerous authors. It was coded as - in *Platanista* which lacks vestibular sacs; 0 for those genera with unfolded vestibular sac (primitive condition), and 1 for *Phocoena* and *Neophocaena*, with folded sacs.

3. Hypertrophied right vestibular sac. Schenkkan (1973) and Heyning (1989) noted this specialization of the river dolphins (except *Platanista*). It was coded - for *Platanista* without vestibular sacs, 0 for those with symmetrical sacs (primitive) and 1 for *Inia* and *Pontoporia*.

4. Orbit in front of nares. Miller (1923) noted this feature in *Monodon* and *Delphinapterus*; it occurs in all the river dolphins. It appears to be present in *Physeter* (van Beneden & Gervais 1868-79; Kellogg, 1928), but not in *Kogia simus* (Perrin pers. comm.) It is not so in extant ziphiids, but it is in *Squaloziphius*, which was considered to be a ziphiid by de Muizon (1990) (but see Fordyce & Barnes, 1994).

Miller (1923) noted the posterior opening of the antorbital canal near the anterior of the orbit in delphinids (based on *Delphinus*), as in terrestrial mammals. Since the antorbital canal was more posterior in those species where the orbit was in front of the nares, he argued that this was the specialized condition. However, the posterior opening of the antorbital canal may also be situated more posteriorly relative to the orbits in phocoenids and *Pseudorca*, which do not have the orbits in front of the level of the nares (pers. obs.). This compromises Miller's argument and the polarity remains equivocal. In the juvenile narwhal UBC 9467, the orbit was already anterior to the nares, so there is no indication of the polarity state from this ontogeny.

Polarity is equivocal based on outgroup analysis, comparative anatomy and ontogeny. The more anterior position of the orbit is considered primitive based on river dolphins and physeterids, and possibly ziphiids (the last based on *Squaloziphius*, which Fordyce & Barnes (1994) considered 'more reminiscent of' the Eurhinodelphidae than Ziphiidae). If they are right, orbit in front of the nares may be a primitive feature by outgroup analysis since the Eurhinodelphoidea is a possible sister group to the Delphinida sensu de Muizon. Coding the anterior position of the orbits as primitive makes the fewest assumptions about the relationships of the river dolphins and monodontids .

5. Separation of pterygoids

Physeter, Berardius and *Platanista* all have medially appressed pterygoids, and by outgroup analysis this is considered the primitive state. Separation of pterygoids is coded as 1.

The palatines and vomer in *Orcaella* resemble those in delphinids where there has been a compression of the palatines and median vomerine spine by the pterygoids. It therefore may not be homologous with the situation in phocoenids, monodontids and some primitive delphinids. All species with widely separated pterygoids are nonetheless scored 1.

6. Posterior nasal sac

We accept Heyning's (1989) argument that a posterior nasal sac is primitive. Its occurrence in the narwhal is from Huber (1934), but Heyning confirmed it in *Delphinapterus*. We have not been able to confirm the loss of this sac in *Sousa*, but it is scored as lacking the sac, as this is a consistent feature of delphinids examined.

7. Mandibular symphysis length

Usually expressed in binary form (short/long) but animals examined fell into 3 ranges: >50% mandible length (in *Physeter* and the river dolphins), 30-50% (*Sousa* and *Steno* (Perrin pers. comm.)) and <30%. The polarity is equivocal by outgroup analysis, as *Physeter* has an elongate mandibular symphysis, but it is shorter (<50%) in *Kogia* and <30% in ziphiids. Coding is 0 =>50%, 1=30-50% and 2=<30%, but since all characters were treated as nonadditive no direction of specialization is implied.

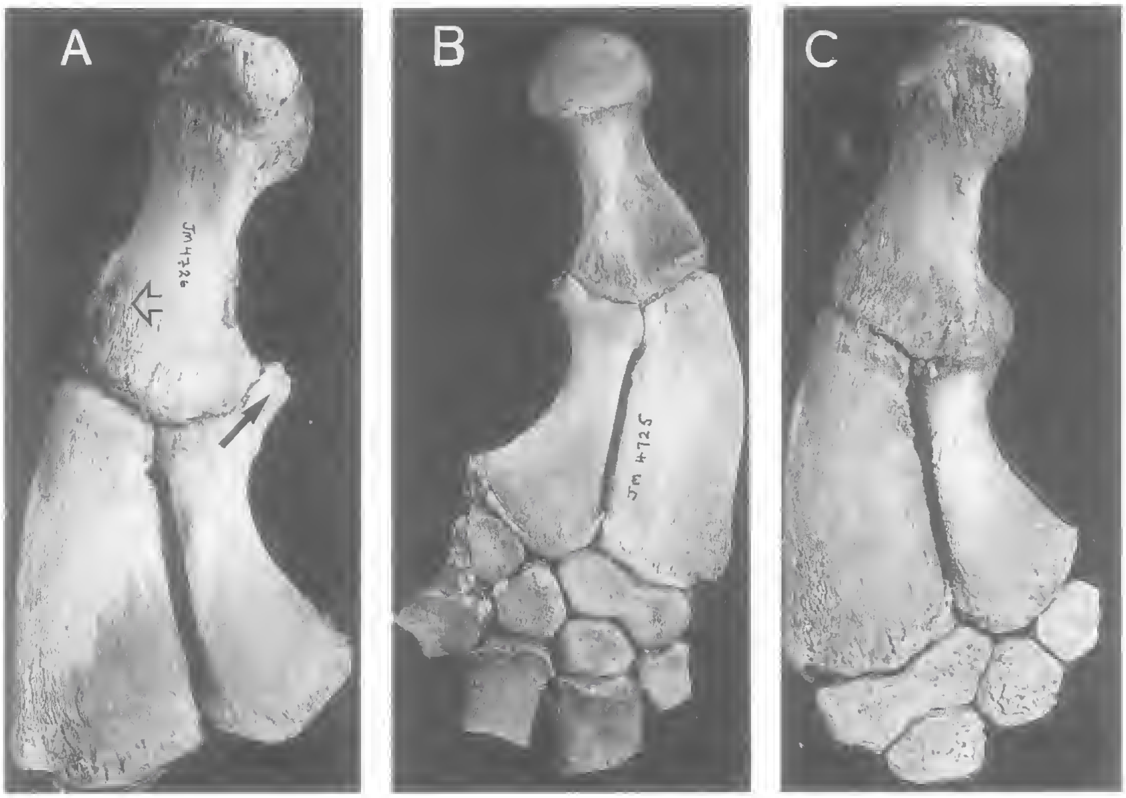

FIG. 48A-C. Variability in development of olecranon process (arrow, in A) in 3 specimens of *Orcaella* from central Queensland. Note the well-developed process in A,B. Also note the elongate deltoid tuberosity of the humerus (open arrow in A).

8. Rostrum length

An elongate rostrum (>60% skull length) was considered primitive, by outgroup analysis. A wide range of fossil odontocetes also have an elongate rostrum. *Neophocaena* has a particularly short rostrum (<40%), while all other genera considered in this study are in the 40-50% range. All are coded 1, however, to reduce the comparisons to binary values. As discussed elsewhere, this feature seems particularly subject to convergences and possible reversals.

9. Atlas and axis separate

The polarity of this character is equivocal by outgroup analysis. *Physeter* has a unique arrangement, where the atlas and axis are separate, but cervicals 2-7 are fused. Extant ziphiids have at least 3 cervicals fused, including the atlas and axis. However, de Muizon (1988) noted that most Mio-Pliocene cetaceans had separate cervicals. This implies that there may have been reversals in some lineages (separate cervicals to partially fused to separate) and thus the character is subject to homoplasy. In the initial analysis, the unfused condition was considered primitive and coded 0 in the analysis. Where only the atlas and axis are fused, the character is coded as 1, while it is 2 for cases when 3 or more cervicals are fused. This extent of fusion of cervical vertebrae has been used (e.g. Nishiwaki, 1963) to define families so it is included as a multistate variable. However, we recognize that the number of fused cervical vertebrae is variable even within a species. Fischer (quoted in Tomilin, 1967) noted that in *Tursiops* there could be fusion of the first two, or the third-fourth and fifth, or even the sixth and seventh cervical vertebrae. Rommel (1990) also noted variability in fusion of the cervicals but attributed at least some of the fusions to pathological conditions. There will also be variability when animals of different ages are compared.

10. Olecranon process

This process on the ulna is considered primitive by outgroup analysis. It is present in ziphiids, although it is less developed in *Berardius* than in *Mesoplodon*, *Ziphius* and *Hyperoodon* (True, 1910; Tomilin, 1967). It is well-developed in *Physeter*, baleen whales and many fossil taxa. The loss of the olecranon (e.g. in *Delphinapterus*, *Monodon*: Tomilin, 1967) must then be considered a derived feature. However, the olecranon process appears variable even among the delphinids and phocoenids; this may be another feature subject to reversals, i.e homoplasy.

de Muizon (1988) considered that *Orcaella* lacks an olecranon process, as in monodontids. Our more extensive series of specimens shows that although the process may be obscure (Fig. 48C), it is generally well-developed (Fig. 48A,B). This is not simply an age dependent feature, as specimens with an olecranon process had 9 and 17 dentinal layers in the teeth.

11. Convex facial profile

This is a specialized feature of extant monodontids and some phocoenids (Perrin, pers. comm.). It is considered a derived feature, as by de Muizon(1988), Heyning (1989) and Barnes (1990). de Muizon (1988) and Marsh et al. (1989) noted that *Orcaella* has a concave supracranial profile, as in delphinids, but unlike monodontids. This argument is weakened by lack of a convex facial profile in the fossil monodontid *Denebola brachycephala* Barnes,1984 and juvenile *Monodon* (Eales, 1950; pers. obs. UBC9467). The latter point is relevant, given the retention of numerous juvenile characters in the skull of *Orcaella*.

12. Premaxillary boss

This is generally recognized (e.g. Rice, 1984; Heyning, 1989) as a specialized feature of phocoenids and is so coded.

13. Bony lateral lamina of pterygoid

This is equivocal by outgroup analysis as the Physeterida (Ziphiidae and Physteridae) shows a reduction in the lateral lamina overall. The bony lamina of the pterygoid is present in *Platanista*. Consideration of fossil cetaceans demonstrates a reduction from a bony lamina as the primitive condition to an increasing development of a membranous lamina (Oelschlager, 1990; de Muizon, 1988). More particularly, the bony lamina is found in fossil platanistoids and in the Eurhinodelphoidea (de Muizon, 1988), a possible sister group to the Delphinida. It is coded, with 0 where the bony lamina is well developed and 1 where it is reduced (in *Phocoena*, fide Fraser & Purves (1962) but not confirmed in the small series of *Phocoena* we examined) or absent. This feature may be particularly variable within the phocoenids (Perrin pers. comm.).

14. Pneumatised maxillary crest

This is a specialized feature of *Platanista* and fossil relatives (Heyning,1989; de Muizon,1990).

15. Palatines covered by pterygoids

This is a specialized feature of *Platanista* (Heyning, 1989). It is a special case of the more general trend for separation of the lateral and medial lobes of the palatine by the pterygoid, also seen to a lesser extent in some individuals of *Berardius* and *Kogia* (de Muizon, in press), as well as *Orcaella, Globicephala* and juveniles of other genera, e.g. *Feresa*.

16. Acquisition of lateral lamina of palatine

This character, used to define the Delphinida by de Muizon(1988), is a specialized feature associated with excavation of the palatine by the pterygoids.

17. Nasopharyngeal sac

This is a specialized feature of *Platanista*. No analagous structure has been documented in other odontocetes, although Anderson (1879) noted what he thought was a rudiment of this structure in a foetal *Orcaella*.

18. Pterygoid sinus undivided

Fraser & Purves (1962) illustrated the cranial sinuses in a variety of odontocetes and used the variations in its development as a basis for classification of cetaceans. The undivided sinus was considered a feature of physeterids and ziphiids (including *Berardius*, although that genus was not included in their summary fig. 22) and *Platanista*. This is the primitive condition by outgroup analysis.

Fraser & Purves (1962), de Muizon (1988) and Heyning (1989) noted the undivided pterygoid sinus in *Delphinapterus* and *Monodon*. This condition is even more primitive than that in river dolphins *Inia* and *Pontoporia*, in which there are distinct pre- and post-orbital lobes (Heyning, 1989). It was the basis for placing the monodontids in their own superfamily Monodontoidea (Fraser & Purves, 1962) and presents difficulties in interpretation (de Muizon, 1988; Heyning, 1989). The latter author, while retaining the monodontids in the superfamily Delphinoidea, commented 'I am perplexed as to how such a primitive air sinus system could have evolved within the Monodontidae'. de Muizon (1990), who considered both fossil and extant taxa, noted that if the condition in monodontids was considered primitive, then reversals would have to be invoked in the Eurhinodelphoids, *Lipotes*, *Pontoporia*, *Inia* and the delphinoids. As with all previous authors, we have had access only to skeletal material, and have inferred the air sinus distribution from this. Although the lateral lamina of the pterygoid makes a particularly convincing boundary in *Monodon* (pers. obs.; see also Pilleri et al., 1982, figs 2b, 3), the extent of the lateral lamina in *Delphinapterus* is more variable. *Pseudorca* shows comparable variation in the development of the bony lateral lamina of the palatine. Purves & Pilleri (1978, fig. 18) illustrated considerable variation in the cranial sinuses of *Pseudorca*, apparently associated with the variation in the bony lateral lamina so there may be comparable variation in *Delphinapterus*. In addition, dissections of specimens have not always confirmed the pattern of sinuses inferred by Fraser & Purves (1962) from the skull, e.g. re-examination of *Inia* and *Pontoporia* by Heyning (1989) resulted in different interpretations of the anterior sinus. It is thus highly desirable that the condition of the cranial sinuses in both *Delphinapterus* and *Monodon* be re-examined by dissection of fresh material. In the absence of such information, we accept the undivided condition of the pterygoids in monodontids as suggested by previous workers and supported by our examination of skulls.

19. Coalescence of pre- and post-orbital lobes of pterygoid sinus to surround optic nerve

Fraser & Purves (1962) documented this as a feature of the delphinids such as *Tursiops, Grampus, Stenella,* and *Delphinus*. Based on their work, deMuizon (1988) used the coalescence of the sinuses as the basis for the subfamily Delphininae, within Delphinidae. This is a specialized feature. Coding is - for those genera which have undivided sinus , 0 for well-separated pre- and post-orbital lobes and 1 for coalescence.

20. Dorsal extension of pre-orbital lobe of pterygoid sinus.

This is a specialized feature of the phocoenids (Fraser & Purves, 1962; Heyning, 1989), but is not shown uniformly throughout the family (Perrin, pers. comm.). There is an incipient extension of this lobe in *Orcaella* (pers. obs.), as already noted by Fraser & Purves (1962) but this is coded as absent in the present analysis, as delphinids such as *Pseudorca* show a similar but less advanced condition. Codes are - for undivided sinus, 0 for limited extension and 1 for well-developed extension of the lobe.

21. Anterior sinus

This is equivocal by outgroup analysis, as the cranial sinus is undivided in ziphiids and physeterids. *Monodon* and *Delphinapterus* would also be coded - as their sinus is undivided. Fraser & Purves (1962) indicated an anterior sinus in *Inia*, based on skull morphology, but Heyning (1989) could not confirm this by dissection. *Inia* is thus coded as 0 (anterior sinus absent) in this analysis. In the absence of contrary information, the configuration indicated by Fraser & Purves (1962) has been accepted. Elongation of the anterior sinus is considered the derived state (Fraser & Purves, 1962).

22. Curvature of flippers

The flippers of mature males of beluga (Vladykov, 1943) and narwhal (Reeves & Tracey, 1980; Martin, 1990) curve upwards at the anterolateral margin. Although this seems a minor character, it is consistent. The deformation of the flipper involves a curvature of the second and third digits (Vladykov, 1943), and may be associated with the relatively larger amount of connective tissue to bone in the flippers of beluga and narwhal than in delphinids. It is a specialized feature of these two genera.

Mature males of both species have a strongly convex posterior edge to the flukes (Vladykov, 1944; Leatherwood & Reeves, 1983); in narwhals the anterior margin may curl forward so that the flukes appear to be 'back to front'. Although there appears to be similar fluke form in the two species, this is not treated as a separate character.

23. Cervical sinus

The indentation of the nape to form a neck-like constriction is a specialized feature, found in *Platanista* (Anderson, 1879), *Inia* (Hoyt, 1984: 68), *Neophocaena* (Hoyt, 1984:75), *Orcaella* and some ziphiids (Perrin pers. comm.).

24. Anterolateral margin of nares formed by maxillaries

This is a specialized feature of extant and fossil monodontids (de Muizon, 1988; Barnes, 1990). de Muizon (1988) pointed out that it is not shared by *Orcaella*, which has the small maxillary intrusions characteristic of many delphinids.

25. Spatulate teeth

This is a specialized feature of phocoenids (Rice, 1984; Heyning, 1989), but variably developed within the family (Perrin pers. comm.).

26. Length of squamosal

Heyning (1989) considered 2 characters associated with the temporal region: roofing over by the frontal bones and length of the squamosal. The length of the squamosal has generally been considered 'short' or 'long'. Examination of a range of genera (from illustrations in the literature as well as examination of skulls) suggested that they form 3 categories : 0-30%, 30-50% and >50%, which are coded as 0, 1 and 2 respectively. Polarity is equivocal by outgroup analysis: *Physeter* is 1 (Miller, 1923), *Berardius* 0 (Tomilin, 1967) and the river dolphins 2. The character is treated as non-additive so no direction of specialization is implied. Heyning (1989) characterized the zygomatic arch of *Orcaella* as 'extremely reduced', a feature he considered a synapomorphy of the delphinids. However, it is about 35% of the cranial vault length in *Orcaella* (pers. obs.) and 39-42% in *Neophocaena*. This approaches the values for *Monodon* (c. 44%) and is much higher than that for delphinids such as *Tursiops* (21-24%) or *Sousa* (23%). Roofing of the temporal region is discussed later (character 39).

27. Disappearance of superior lamina of pterygoid in orbital region

This is equivocal by outgroup analysis; it was considered an advanced character by Fraser & Purves (1962). This is consistent with the reduction of bony margins to the cranial sinuses as indicated by Oelschlager (1990). de Muizon (1988) noted the strongly developed superior lamina of the pterygoid in Platanistoidea and the Eurhinodelphoidea. The superior lamina is thus considered primitive while its disappearance is treated as the derived condition in this analysis.

28. Orientation of posterior process of periotic

The process is oriented strongly ventrad towards the posterior process of the tympanic or posteriorly, except in delphinids where it is posterolateral to strongly lateral (Kasuya, 1973). The latter is considered specialized (coded 2); ventral orientation (*Platanista*) is coded as 0; posterior orientation as 1.

29. Orientation of posterior process of tympanic

Polarity is equivocal by outgroup analysis; the posterior orientation was considered primitive by Kasuya (1973) and is accepted as such here. We observed the orientation of the process in *Orcaella* to be posterolateral, not posterior as indicated by previous authors (e.g. Kasuya, 1973).

30. Sigmoid process of tympanic bulla

Four forms of the sigmoid process are recognized, based on Kasuya (1973) and Pilleri et al. 1989: square (*Physeter*), flail-shaped (*Berardius*), short (river dolphins) and long & L-shaped (all others). In our analysis, the short sigmoid process of the river dolphins was coded 0 and the L-shaped process 1. No direction of specialization is implied and, in any case, the character reduces to a binary feature in the present analysis.

31. Lateral furrow of tympanic bulla

The polarity of this feature is equivocal by outgroup analysis: it is absent in *Physeter* (and *Kogia*), but present in ziphiids and the river dolphins. It is generally present in fossil odontocetes, including most physeteroids (de Muizon, 1988). It is considered primitive, as by Kasuya (1973).

32. Width of posterior branch, lower tympanic aperture of bulla.

The lower tympanic aperture is not present in physeterids, but is less than 10% standard length of the tympanic bone in *Berardius* and all river dolphins except *Pontoporia*. The branch is over 10% in *Delphinapterus* (Kasuya, 1973, based on very small sample size) and phocoenids. The wide branch is considered a specialization, by outgroup analysis, but this is equivocal (see below). Although boundaries set on continuous variables will always be more or less arbitrary, the value of 10% did appear to be relatively well defined. It also is consistent with use by Kasuya (1973), whose study on tympanoperiotic bones has been very influential. Coding is 0 for < 10% and 1 for > 10% standard length of tympanic.

A lateral shift of the posterior process will compress to some extent the posterior branch of the lower tympanic aperture. Thus there may be a purely structural reason for the fact that taxa like phocoenids and beluga, with a posteriorly directed posterior process, have a wide aperture while the delphinids, with postero-lateral to lateral process of the tympanic, have a narrower aperture. Thus this character may not be independent of character 29, and it could be argued that the primitive condition was a wide aperture, associated with a posteriorly directed process (considered the primitive condition, see character 29).

In *Orcaella* the LTA width is <10% (see section on Tympanoperiotic bones).

33. Compression of bulla

Compression of the bulla (width 50% or less of standard length of tympanic bulla) occurs in *Platanista, Monodon* and *Globicephala*. Lack of compression is considered primitive by outgroup analysis.

34. Sutural connection of tympanoperiotic to skull

Heyning's (1989) interpretation is accepted here. There is a sutural connection in ziphiids and physeterids. This is considered primitive. *Platanista* shows an intermediate condition, with partial fusion to the skull, while all others considered show no sutural connection to the skull. This feature may be subject to some variation within species. Kleinenberg et al. (1964) and Kasuya (1973) reported that the periotic was sutured to the skull in *Delphinapterus*, but neither Heyning (1989) nor we found this to be the case on belugas we examined (see discussion of tympanoperiotic bones for further details).

35. Retraction of premaxillaries from nasals

The anterior retraction of the premaxillaries is a specialized feature of phocoenids (de Muizon, 1988; Heyning, 1989; Barnes, 1990). The river dolphins supposedly show a gradation of lateral retraction of the premaxillaries, but this is not coded here because it is difficult to quantify and appears to overlap with retraction in some delphinids. The general condition in which the left premaxilla is retracted away, while the right premaxilla maintains close contact with the nasals, is considered a feature of the delphinids, as by previous authors (e.g. de Muizon, 1988; Heyning, 1989; Barnes, 1990), but it is variable.

36. position of attachment of tympanoperiotic to skull

In *Delphinapterus, Monodon* and *Orcaella*, the dorsal surface of the posterior processes of periotic and tympanic bones are involved in the connection to the mastoid portion of the squamosal. In the phocoenids, which also have a large mastoid portion of the zygomatic arch, and the delphinids, where the mastoid portion is compressed by the exoccipitals, the processes of the tympanoperiotic join in a cavity formed by the basioccipital, exoccipital and squamosal, more dorsally placed than in the three genera just mentioned. The attachment seems to be a distinctly different form in ziphiids and physeterids, however the more ventral attachment is similar to the situation in *Platanista*. The type of attachment in *Delphinapterus, Monodon* and *Orcaella* is thus considered primitive.

37. Profile of tympanic bulla

de Muizon (1988) and Pilleri et al., (1989) indicate that the bulla in outer lateral view may have a convex or concave profile. The former characterizes Physeteridae, Ziphiidae and all the river dolphins; it is thus primitive by outgroup analysis. Monodontids, phocoenids and delphinids have a concave profile.

38. Shape of anterior process of periotic

de Muizon (1988) listed a square, almost rectangular, profile of the anterior process as a character of the Delphinoidea (Monodontidae, Phocoenidae, Delphinidae) and said that it was a consistently recognizable character. Kasuya (1973), however, was less clear in this separation. He noted that the process was curved and rod-like in *Physeter* and *Platanista*, pyramidal in ziphiids (although elongate in *Berardius*), and flat & rectangular in *Inia, Pontoporia, Delphinapterus* and *Monodon*, phocoenids and delphinids. Kasuya's scheme is used here. There may be some variation, however, in the form of the anterior process in *Monodon*: UBC9467 has an elongate, curved process.

39. Roofing of temporal fossa

The outgroup analysis is equivocal in defining polarity. In *Physeter* and *Berardius* it is roofed over, but in some fossil physeterids (e.g. *Diaphorocetus*: Kellogg, 1928) and various fossil taxa (Agorophiidae, Squalodontidae) as well as *Kogia* (Perrin pers. comm.) and the river dolphins it is open, exposing the wide zygomatic arches. Following Heyning (1989), this is considered the primitive state, with roofing of the temporal region derived. It should be noted that the reason for considering the feature primitive is not because it occurs in a fossil species, but because it is present in at least some representatives of the outgroup, which just happen to be fossil species.

CHARACTERS NOT CONSIDERED

Heyning (1989) included a number of characters specific to ziphiids (e.g. throat grooves, elevated vertex) or physeterids (e.g. spermaceti organ, distal sac, lack of one nasal bone). Since the inter-relationships of the Physeteridae and Ziphiidae are not under examination, and these characters are irrelevant to the Delphinida (*sensu* de Muizon, 1988), they have not been included. Additional characters not considered are listed below.

1. Bicipital ribs

Slijper (1936, 1962) considered an elevated number of bicipital ribs as a primitive condition. He envisioned that reduction of bicipital ribs was linked to a need for flexibility of the thorax in a diving mammal (Slijper, 1962). This argument is weakened by the finding of Rommel(1990) that the elastic ligaments allowed significant flexure of the bicipital ribs in *Tursiops*. The number of bicipital ribs (7-8/12-13 ribs) in *Orcaella* (see Appendix 4) is higher than in most delphinids, comparable to *Delphinapterus* (8/11-12: Slijper, 1936) but lower than in phocoenids (11/13-14 in *Neophocaena*; 10/12-14 in *Phocoena*: Nishiwaki, 1963). Insufficient information was available to use this character.

2. Lip on nasal plug

Schenkkan (1973) illustrated the increasing development of a lateral lip on the plug from *Kogia*, *Pontoporia*, ziphiids through to *Phocoena* and delphinids. Insufficient information was available for other genera to use this character. Similarly, there was insufficient information to assess any patterns in the extension of the melon into the right or left nasal plug.

3. Proportion of premaxillary sac to vestibular sac

Schenkkan (1973) documented a gradation from large vestibular sacs in *Pontoporia*, *Inia* and *Phocoena* to small sacs in *Delphinus* and *Stenella*. Conversely, the premaxillary sacs assumed greater relative importance from the river dolphins to *Delphinus* and *Stenella*. We could not calculate values for monodontids or some of the delphinids not considered by Schenkkan, so have not included the character.

4. Coat of cement on tooth

Lonnberg (1910) contrasted the teeth of *Delphinapterus* with those of *Phocoena*, *Steno*, *Globicephala* and *Delphinus*. The former differed from the porpoise and dolphins examined in the strong development of a cement coat, constituting the bulk of the tooth. As pointed out by Lonnberg, a similar tooth structure occurs in *Physeter*, suggesting that this may be the primitive condition. It is not associated with the size of the teeth; *Orcinus* has a typical delphinid tooth. The cement coat on teeth of *Kogia* may be extensive, building up to form a convex profile to the tooth in old animals of both species in the genus (Ross pers. comm.). Among ziphiids, the situation is more variable: in *Hyperoodon* and *Ziphius* most of the tooth is cement, but dentine predominates in teeth of *Berardius* (Ross pers. comm.). *Platanista* has a substantial cement component in the teeth, but Kasuya (1972) noted that it is distinct from the pattern in *Physeter*. A cement coat extends the entire length of the erupted tusk in *Monodon* (Reeves & Tracey, 1980) but it is unclear if it is as well developed as in *Delphinapterus* or *Physeter*. There were insufficient data to establish polarity of the character, either by outgroup analysis or other arguments. A similar situation exists for accessory cusps, which occur in juvenile *Delphinapterus* (Stewart & Stewart, 1989) and are sporadic in other odontocetes.

5. Phalangeal formula and flipper shape

de Muizon (1988) noted that there is a greater number of phalanges in digits 2 and 3, relative to the other digits in delphinids, whereas there is greater uniformity in monodontids. However, a comparison of phalangeal formula for *Delphinapterus*, *Monodon* and various dolphins suggest there is considerable overlap. In particular, the formula is similar in *Orcinus* (I:2; II:6-7; III:4-5; IV: 3-4; V: 2-3: Nishiwaki, 1963)to the monodontids (*Monodon*: I:1-2; II: 5-8; III: 4-6; IV:2-4; V: 2-3; *Delphinapterus*: I:1-2; II: 6-9; III: 4-5; IV:2-4; V: 2-4: Nishiwaki, 1963). Eales (1953) noted that phalangeal number decreases with age in the narwhal and beluga; the curvature of the flipper in adult males may be related to this fact. However, it can not be used as a character for the monodontids, as this reduction was also found in *Phocoena* (Eales, 1953). The flipper does tend to be more squared-off in *Physeter*, ziphiids, platanistids and monodontids, than it is in phocoenids and delphinids, but there is variation in form among the latter (e.g. *Orcinus*, a delphinid, has broad paddle-shaped flippers especially developed in the male).

6. Position of delto-pectoral tuberosity

de Muizon(1988) considered the distal position of this tuberosity a feature of delphinids and phocoenids. He further indicated that the tuberosity was subdistal in *Orcaella*, linking it more with the monodontids. On our specimens (Fig. 48 A,B,C), the tuberosity was elongate and, while not distal, it was not as clearly subdistal as figured for *Delphinapterus* and *Monodon* by de Muizon (1988, fig. 22).

TABLE 6. External morphometrics for 22 specimens of *Orcaella brevirostris* from central Queenland. Numbers in the left hand column refer to the following measurements. Values for 2-17 are percentages of total length. 1. Total length (m); 2. Tip of upper jaw to eye; 3. Tip of upper jaw to gape; 4. Tip of upper jaw to ear (auditory meatus); 5. Length eye to ear; 6. Tip of upper jaw to anterior base flipper; 7. Tip of upper jaw to blowhole; 8. Tip of upper jaw to tip of dorsal fin; 9. Tip of upper jaw to umbilicus; 10. Tip of upper jaw to genital aperture (centre); 11. Tip of upper jaw to anus; 12. Length of anterior margin flipper; 13. Length flipper from tip to axilla; 14. Maximum width flipper; 15. Height dorsal fin; 16. Length of dorsal fin base; 17. Width of tail flukes.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0.91	1.05	1.34	1.86	1.87	2.11	2.12	2.12	2.12	2.14	2.15	2.15	2.15	2.17	2.19
2	11.54	11.40	9.20	6.70	9.63	7.10	-	6.10	6.10	6.80	7.90	7.00	7.40	5.50	7.30
3	9.34	10.70	7.60	5.60	8.60	6.60	-	4.70	4.30	5.60	7.44	5.60	5.60	4.60	5.00
4	15.71	-	13.30	10.40	-	-	-	7.80	12.30	-	12.10	10.00	11.20	8.80	11.40
5	5.05	-	4.30	-	-	-	-	3.10	6.10	-	3.30	3.49	4.00	3.20	4.10
6	24.73	22.90	23.20	19.60	23.00	17.50	-	18.90	17.90	20.10	19.50	18.60	18.60	16.10	18.30
7	9.78	11.90	11.50	6.10	10.16	7.60	-	3.77	5.70	5.15	6.50	6.50	11.20	8.30	11.40
8	57.14	60.00	58.20	57.50	62.60	-	-	55.20	59.40	54.80	57.00	54.90	58.10	57.60	63.00
9	47.80	48.60	44.50	-	44.90	-	-	-	-	44.50	44.20	42.30	44.70	42.40	-
10	63.19	55.20	60.70	60.50	60.40	-	-	56.60	52.40	-	61.60	54.90	54.40	63.60	54.34
11	65.60	66.70	64.40	64.20	64.20	-	-	66.50	60.80	66.50	66.50	66.50	64.20	67.70	64.80
12	20.33	20.00	17.40	16.40	17.10	17.10	15.10	17.90	15.60	15.90	16.70	18.80	19.80	16.60	16.00
13	18.13	15.90	13.60	12.60	13.90	13.70	12.30	14.40	13.70	15.40	14.90	16.70	16.30	15.20	14.20
14	7.69	7.90	5.80	6.60	6.40	5.90	-	6.80	5.90	7.00	7.20	7.00	7.40	7.40	6.80
15	3.85	5.20	3.70	4.00	4.30	-	-	-	3.80	4.70	4.40	5.10	5.10	5.30	4.60
16	7.69	-	10.10	7.50	9.60	13.30	-	7.60	5.40	9.80	10.20	7.90	7.40	8.10	9.10
17	18.68	27.10	21.40	29.00	25.10	23.70	-	31.60	26.40	33.20	30.20	32.30	30.70	24.90	35.60

7. Impression of 'duplicated apex of nasofrontal sac' on skull

de Muizon (1988) documented fosetta or shallow depressions on the anterior face of the brain case above the nares in phocoenids and monodontids. He considered these the impressions of a duplicated apex of the nasofrontal sacs (apparently the same as the 'posterior nasal sac' of Heyning, 1989). We noticed similar fosetta in *Orcaella* but there was no indication of a posterior nasal sac in our dissections of *Orcaella* (see Facial Anatomy). We therefore reject the occurrence of such fosetta as evidence for a posterior nasal sac.

8. Development of mesethmoid plate and elevation of nasals

de Muizon (1988) and Barnes (1990) linked these two characters, which they considered diagnostic of delphinids. *Orcaella* examined herein have a poorly developed mesethmoid plate, which does not impinge on the reduced nasals. However, the nasals are still elevated on the vertex, suggesting that the characters are not linked. Elevation of the nasals may be a more consistent character for the delphinids, although there are similarities in the position of the nasals in *Monodon*, *Delphinapterus* and the delphinid *Pseudorca*. These characters are supporting features of the delphinids but are not incorporated in the analysis, because of their variability (even between populations of *Orcaella* in the case of the development of mesethmoid plate).

9. Compression of vertebral centra

de Muizon (1988) suggested that delphinids showed a tendency for compression of the vertebral centra. This is linked to higher numbers of vertebrae, and possibly a greater flexibility of the spinal column. Low numbers of vertebrae (under 60) does appear to be a primitive character (see Table in Watson, 1985), but quite unrelated species show elevated numbers of vertebrae (e.g. *Phocoenoides* among phocoenids, *Lissodelphis* and some *Lagenorhynchus* in delphinids). Due to this variability, the feature was not included.

Similarly, de Muizon (1988) suggested that the Phocoenidae and Delphinidae have more elongated transverse processes of the lumbar vertebrae, contrasted with more triangular processes in other Delphinida, such as river dolphins (except *Platanista*) and *Delphinapterus*. However, there again seems to be much variation in delphinids. The transverse processes of a North Atlantic *Globicephala melas* are intermediate between those of *Delphinapterus* and delphinids

TABLE 6 (continued)

	16	17	18	19	20	21	22
1	2.19	2.20	2.22	2.25	2.25	2.26	2.35
2	-	6.40	5.90	8.40	6.20	9.10	6.80
3	-	5.20	4.50	5.80	5.30	7.10	5.10
4	-	12.00	-	10.70	12.00	4.90	10.60
5	-	7.30	-	4.00	-	3.50	3.80
6	19.20	18.20	18.50	19.60	17.30	19.90	19.20
7	-	5.50	5.40	7.10	7.60	11.10	11.50
8	58.50	56.80	56.80	56.00	56.40	53.10	56.60
9	-	42.70	-	-	44.90	36.70	42.60
10	61.60	54.50	-	-	63.10	51.30	53.20
11	64.40	65.20	66.20	-	65.80	54.00	64.70
12	-	19.10	16.70	16.90	17.80	17.30	15.70
13	-	16.10	14.00	16.40	16.00	12.80	14.00
14	-	7.50	5.80	7.10	6.70	6.60	6.20
15	-	4.80	3.60	4.40	4.00	4.40	3.40
16	-	8.20	6.30	8.90	7.10	8.40	7.70
17	28.80	34.00	26.10	29.80	-	24.80	26.00

such as *Lagenorhynchus acutus* with elongate processes (pers. obs.).

10. Palatine bridge under optic channel

de Muizon (1988) considered this a feature of the monodontids; we observed it in beluga and, even more strikingly so, in narwhal but have not used it as a character because posterior development of a palatine wing is not restricted to monodontids. It is equally developed in the delphinid *Pseudorca*, where the lateral boundary is formed exclusively of palatine bone which extends almost to the squamosal. The posterior extension of the palatine, in combination with the more anterior position of the orbit in monodontids, is the basis for the obvious bridge underlying the optic channel in *Delphinapterus* and *Monodon*. It is particularly striking in the latter because of the strong depression of the skull in that genus;this ensures that the palatine wing is closely appressed to the optic channel. *Orcaella* represents the opposite extreme where the posterior extension of the palatine extends outward, well away from the basicranial bones, as a free wing-like structure.

Since we consider the palatine bridge to be associated with the more anterior position of the orbits (character 4), we do not include the palatine bridge as a separate character.

11. Immunological and electrophoretic distance

Lint et al. (1990) demonstrated a close relationship of *Monodon* with *Delphinapterus*, based on immunological distance; *Orcaella* was well separated from these genera and grouped with the delphinids, *Orcinus* and *Lagenorhynchus*. *Inia* was closer to the monodontids than delphinids, but was not closely linked to either. These relationships were supported by electrophoretic data, and combined with the latter to give a phylogeny of odontocetes (Lint et al., 1990: fig. 2d) in which delphinids were widely separated from phocoenids. These data have been discussed elsewhere, but were not used in our analysis because there were insufficient data for all species.

12. Base pair length of repetitive DNA

Gretarsdottir & Arnason (1992) compared the base pair lengths of highly repetitive DNA in a variety of odontocetes. Representatives of most families examined, including beluga and narwhal, had a primitive base pair length of about 1750 bp. The delphinids, however, had a bp length of about 1580, while *Orcaella* had a base pair length of 1583.

These data support *Orcaella* being a delphinid, but could not be incorporated in the analysis because comparable data were not available for other species; most importantly there were no data for any of the river dolphins.

13. Isovaleric acid and acoustic fat

Litchfield et al. (1975) compared odontocetes for distribution of lipids in both acoustic (melon and mandible fatty bodies) and non-acoustic (e.g. blubber) tissues. They separated two groups: ziphiids, physeterids and 'Platanistidae' (*Platanista,Inia*) without isovaleric acid in the acoustic tissue, and the Monodontidae, Phocoenidae and Delphinidae with isovaleric acid. They further subdivided the latter group, with delphinids having over 3% of the lipids as waxy esters, while the monodontids and phocoenids had exclusively triglycerides.

Morris (1985) argued that isovaleric acid can not be considered a by- or waste product of standard physiological processes but represents a specialization, produced at considerable physiological cost. Presence of isovaleric acid has been linked to development of the melon, and the function of fat in the melon as an acoustic lens. As pointed out by Litchfield et al (1975), some other mechanism must be used by the river dol-

TABLE 7. External morphometrics for 11 specimens of *Orcaella* from SE Asia. Numbers in the extreme left hand column are measurements, as in Table 6. Specimen numbers 1, 3, 5, 7 & 10 are from Anderson (1879); 2, 6, & 9 from Tas'an et al., 1980; 4, 8 & 11 from Pilleri & Gihr, 1973-1974.

	1	2	3	4	5	6	7	8	9	10	11
1	0.86	1.53	1.80	1.93	2.10	2.11	2.19	2.20	2.20	2.29	2.75
2	-	9.80	-	8.80	-	8.53	-	-	-	-	-
3	6.70	-	8.00	-	7.3	-	5.88	-	-	6.40	-
4	-	14.70	-	-	-	13.30	-	-	-	8.90[9]	-
5	-	2.00	-	-	-	3.30	3.50	-	-	4.20	-
6	23.00	26.80	22.20	21.20	20.00	19.90	-	23.9[8]	-	20.80	38.20[8]
7	-	9.80	12.80	9.80	12.10	9.50	-	-	10.90	11.10	-
8	53.30[1]	54.90	59.20[2]	56.00	55.80[2]	49.30	56.90[4]	57.40[8]	60.40	61.90[2]	66.50[8]
9	49.60	65.40	-	-	-	55.00	-	-	-	-	-
10	62.90	68.60	-	-	-	62.60	-	-	-	58.60	-
11	-	71.90	-	-	-	-	73.20[5]	67.60[8]	-	-	74.50[8]
12	23.70	19.00	22.20	14.50[3]	20.60	11.80	17.40[6]	17.50[3]	-	18.90	15.00[3]
13	-	-	16.20	-	14.50	-	-	-	-	13.00	-
14	-	5.20	8.10	6.20	7.60	9.50	7.03	-	-	-	-
15	-	2.90	3.20	2.30	4.50	2.40	2.40[7]	2.90	3.20	7.0310	2.50
16	-	13.10	7.04	5.70	9.69	10.40	10.40	6.60	-	5.30	6.60
17	-	26.10	28.20	25.40	26.10	30.80	27.90	27.30	29.50	-	23.90

Notes:- 1. to anterior of base; 2. curved along back; 3. unspecified flipper length; 4. to middle of fin; 5. calculated by subtraction of published values; 6. in centre of flipper; 7. 'depth through center'; 8. indirectly calculated; 9 to anterior of eye; 10. 'anterior of base to posterior of tip'.

phins, but distribution of isovaleric acid suggests that it is a derived feature of the more specialized delphinoids. It was not used in the analysis because of missing values for a number of species.

14. Pseudaliid nematode parasites

At least 28 nominal species of pseudaliid nematodes have been reported from the cranial sinuses and respiratory tract of odontocetes and they are perhaps the most promising group of parasites to use in assessing inter-relationships of the hosts.

Except for *Delamurella* Gubanov, 1952 in *Berardius* from the northwest Pacific, pseudaliids are restricted to the Delphinida sensu deMuizon (1988). This record is apparently based on a single report; more information is necessary to evaluate the relationship of *Delamurella* to other pseudaliids.

The phocoenids have the widest range of pseudaliid parasites: *P. phocoena* has 5 species, *Phocoenoides dalli* 6 and *Neophocaena phocaenoides* 5 nominal species, with limited overlap of parasites between host species. *Pseudalius* is apparently restricted to phocoenids (but see anomalous records below). Arnold & Gaskin (1975) maintained *Torynurus* Baylis & Daubney, 1925 distinct from *Pharurus*; at that time the genera were known from phocoenids (*Phocoena, Phocoenoides*) and monodontids respectively. Descriptions of additional species from *Neophocaena* and *Phocoenoides* (Petter & Pilleri,1982; Kuramochi et al.,1990) have blurred distinctions between these genera. The diagnostic characters of *Pharurus, Torynurus, Stenurus* and *Pseudostenurus* need to be re-evaluated; study of new material of *Pseudostenurus* from *Neophocaena* is crucial to such a review. The species of *Halocercus* in *Phocoenoides* and *Neophocaena* also need review.

If the restricted definition of *Pharurus* as proposed by Arnold & Gaskin (1975) is confirmed, then this genus is restricted to monodontids (*P. pallasi* in *Delphinapterus, P. alatus* in *Monodon*). The other genera reported from monodontids (*Stenurus, Halocercus*) have also been reported in phocoenids and delphinids.

Identifications of pseudaliids in delphinids are often incomplete and poorly documented. *Delphinus delphis* has the largest number (4) of pseudaliid species reported from any delphinid host, all in *Halocercus* or *Skrjabinalius*; some of these species require confirmation. *Halocercus* and *Skrjabinalius* have the widest reported distributions within the Delphinidae, having been reported from *Delphinus, Stenella, Tursiops, Lagenorhynchus, Sotalia, Sousa, Peponocephala* and *Cephalorhynchus. Skrjabinalius* is known only in the Delphinidae. Distinctions between the species of *Halocercus* in particular are often poorly documented and many records need confirmation. *Stenurus ovatus* has been recorded in *Tursiops* and *Lagenodelphis,* while *S. globicephalae* has been reported from *Globicephala melas, G. macrorhynchus, Lagenorhynchus acutus, Grampus griseus, Peponocephala electra* and *Feresa attenuata.* Unidentified species of *Stenurus* have been reported from *Cephalorhynchus hectori* and *Lissodelphis peronii.* No pseudaliids have been reported from *Orcinus* or *Orcaella*, nor have we found any pseudaliids in the *Orcaella* we necropsied.

Analysis at species level is complicated by the probability of misidentifications in the literature, as noted above. For instance, *Stenurus minor* has been reported from *Delphinapterus leucas, Phocoena phocoena, Phocoenoides dalli* and *Grampus griseus.* The last record is based on a single report by von Linstow (1910). This predates the description of *Stenurus globicephalae*, which is well-known from various blunt-headed genera, including *G. griseus* (Arnold & Gaskin, 1975; paragraph above). Additional questionable or anomalous records include *T. convolutus* and *Pseudalius inflexus* in *Lagenorhynchus acutus* and *Pseudostenurus auditivus* in *Pseudorca.*

Until necessary revision is done on pseudaliids and questionable records evaluated, the distribution of pseudaliid parasites in odontocetes offers little help in assessing inter-relationships of the hosts.

APPENDIX 3: EXTERNAL MORPHOMETRICS

RESULTS

General features correspond well with descriptions of *Orcaella brevirostris* from Anderson (1879), Lloze (1982) and Marsh et al. (1989).

Among 37 animals from central Queensland, the longest ♂ is 2.70m , the next longest being 2.35m. The longest ♀ is 2.30m; two animals of unknown sex are 2.35 and 2.49m long.

Body proportions are available for a smaller sample (19 animals 1.86-2.35m and 3 animals 0.91-1.34m long). These are compared with measurements in the literature (Tables 6 & 7). There are anomalous values for animal 21 (Table 6); the measurements are not used in the calculation of the descriptive statistics.

Dimensions of the head (e.g. rostrum to eye, rostrum to flipper, rostrum to gape, rostrum to auditory meatus) are larger in the small animals (0.91-1.34m total length). The only clear sexual dimorphism is in the more posterior position of the genital aperture in ♀♀ (61.6-63.6% total length, plus one anomalous value of 54.9%) than in males (52.4-56.6%). Even with the anomalous value included, the difference is statistically significant (5%, Mann-Whitney U test). There was almost total overlap between sexes for all other characters.

There is considerable variability in the measurement of the dorsal fin base, which is difficult to clearly define. The wide variation in fluke widths may reflect post-mortem shrinkage in some of the stranded animals, as well as errors introduced by calculating total width by extrapolating from one undamaged fluke.

DISCUSSION

Our data and other records (e.g. Pilleri & Gihr, 1973-1974) suggest that ♂♂ grow larger than ♀♀, but the numbers of animals examined is small. More material is necessary to confirm the possible sexual dimorphism in body length.

Morphometrics for 11 SE Asian specimens were collated from the literature (Table 7). For our comparisons, we do not separate *O. 'fluminalis'* and *O. brevirostris.* Smaller animals (0.91-1.34m long) are considered separately.

Animals from Indonesia measured by Tas'an et al. (1980) had much higher values for the measurement 'tip of upper jaw to the umbilicus' than all animals from Queensland. This feature was not routinely measured by other authors, however Lloze (MS) noted that in two specimens 1.9 and 2.0m long from the Mekong, the umbilicus occurs '5-6cm in front of the midlength of the body'. This gives a figure of approximately 47% total length, which is consistent with the Queensland sample. Thus the values reported for Indonesian animals do not necessarily indicate variation between Queensland and SE Asian animals.

Some measurements appear to be taken in different ways. The distance between upper jaw and blowhole will vary according to whether it is taken in a direct line (using calipers) or curved over the body. The measurement of the dorsal fin base also seems to be subject to wide variation. Published values for flipper length (Table 7) were measured along the anterior margin, through the

TABLE 8. Length-weight data for *Orcaella brevirostris*, combining original data from Queensland with literature records. The record from Anderson, 1879 was a near term foetus from India. The records from Tas'an et al., 1980 were consecutive weighings of a captive Indonesian animal. Records of Lloze were from the Mekong River. *= the animal was weighed in pieces, so weight is underestimated.

LENGTH (m)	WEIGHT (kg)	SOURCE
0.86	10.4	Anderson, 1879
0.91	9.9	original
0.96	12.3	Tas'an et al., 1980
1.26	30	Tas'an et al., 1980
1.34	30.9	original
1.53	45	Tas'an et al., 1980
1.90	80	Lloze in Marsh et al., 1989
2.00	87	Lloze in Marsh et al., 1989
2.14	114	*original
2.15	127.9	*original
2.17	190	Marsh et al., 1989
2.25	132.9	*original

centre of the flipper or at an unspecified location. In spite of these inconsistencies, there is general agreement in proportions of animals over 1.86 m long, although the 2.75m male from Thailand (Bonhote in Pilleri & Gihr, 1973-1974) had anomalously high values for rostrum to flipper and rostrum to dorsal fin, as well as a low value for fluke width. Height of the dorsal fin is consistently higher (4.4% (3.4-5.3%), n=18) in Queensland animals, compared with the SE Asian animals (2.9% (2.3-4.5%), n=9); this is highly significant (p =0.002%, Mann-Whitney U test). The 'height' of the dorsal fin in a 2.29 m ♂ (Anderson,1879) was 7.03% (Table 7), however the measurement was taken from the anterior of the base of the fin to the posterior tip of the fin. This implies that it was an oblique measurement, not comparable to the standard height, and the value is not included for comparison. The dorsal fin of Qld animals appears higher, with a more convex anterior margin and shorter base than animals from Kalimantan held at Jaya Ancol Oceanarium (based on photos taken by Dr A. Preen). The posterior margin of the fin of Qld animals is also much straighter (Fig. 3) than the distinctly emarginate border illustrated by Anderson (1879, pl. 25, fig. 4), and is closer to the 2.2 m ♂ *O. 'fluminalis'* illustrated by that author (pl. 25a, fig. 1). In Qld specimens the tip of the fin is usually acute, however it could be rounded as in some SE Asian animals (e.g. Lloze, 1982, Fig. 1).

General accounts (e.g. Morzer-Bruyns, 1971; Sylvestre, 1993) of the Irrawaddy Dolphin give the average weight as 100 kg; Martin (1990) noted that 'typically' weight was 90-150kg. There appear to be very few published values of weights (Table 8). The weights of three animals from Qld between 2.14-2.25m long varied between 114-133kg.

These are underestimates as the animals were weighed in pieces, with loss of body fluids and blood. Another animal 2.17 m long, also weighed in pieces, was reported to weigh 190 kg (Marsh et al., 1989). This value was confirmed from the original data sheets, but in light of other measurements, appears to be too high. More data are needed to provide an accurate length-weight relationship.

APPENDIX 4: POST-CRANIAL SKELETON

AXIAL SKELETON

The vertebral formula for 6 central Qld specimens is C7, T12-13, L9-12, Ca28-30 = 58-60, with 17-20 chevrons and up to two nodules below the caudals. In JM511, there is a small tubercle on the last caudal vertebra; if this represents a fused vertebra the total count becomes 61.

CERVICAL VERTEBRAE (Fig.49)

The first 2 cervical vertebrae are fused. The combined neural processes of C1-C2 are usually bifid at the top (Fig. 49). The transverse processes of C1-C2 are low tubercles, barely extending beyond the condylar facets in anterior view (Fig. 49A). The condylar facets are well separated ventrally.

Diapophyses and parapophyses are developed to a variable degree on cervicals 3-7; in QMJM 4729 (MM92) they are obvious only on cervical 4 (Fig. 49A,B). The last cervical vertebra is distinct in its high neural process, well developed transverse processes and costal facet on the centrum.

THORACIC VERTEBRAE (Fig. 50)

The anterior eight thoracic vertebrae are of similar width; the transverse processes increase in width from T8, with the last thoracic vertebra distinctly wider than the others. On several specimens the anterior border of the transverse processes of the last thoracic vertebra has a distinct antrorse spine (Fig. 50B). In QMJM511, the transverse processes of the last (12th) thoracic vertebra have distinct facets for articulation with the ribs. MM333 has 13 thoracic vertebrae, each with a fossa or swelling of the tip of the transverse processes.

The first metapophysis appears on T7-8 ; the

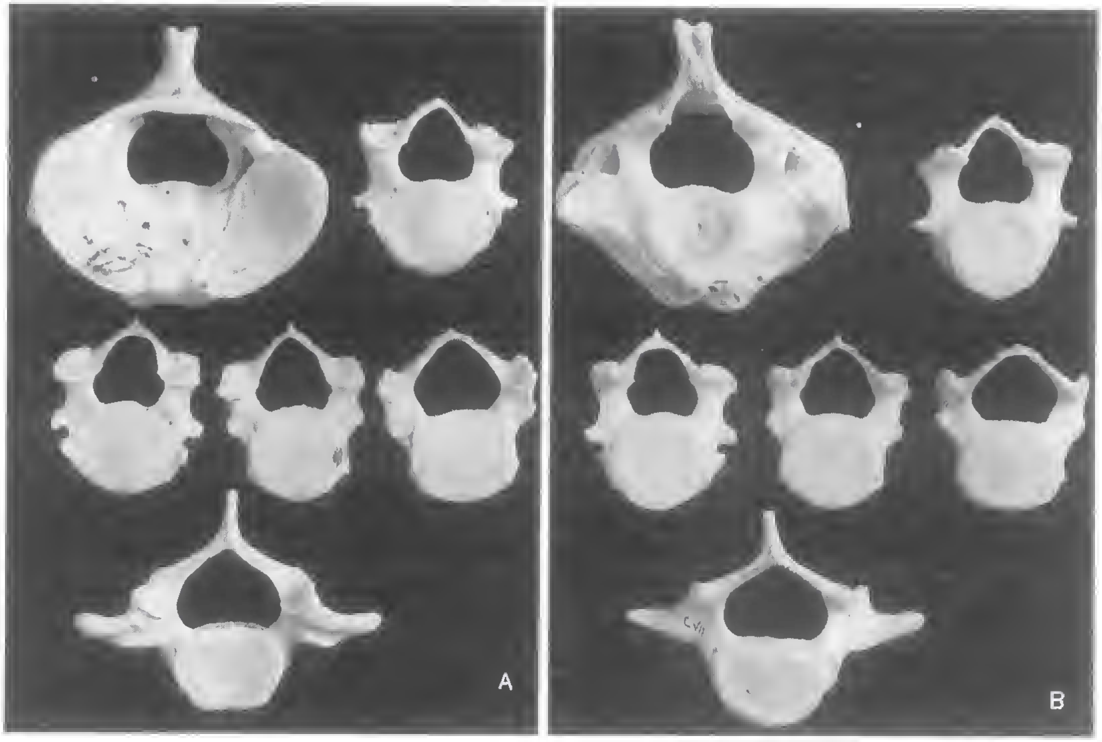

FIG. 49. Cervical vertebrae of QMJM4729, a 2.12 m long ♂. A, Anterior view. B, Posterior view. Note bifid spinous process and poorly developed transverse processes of fused cervicals 1 & 2.

last postzygopophysis on T8-9. The last costal facet is on T7.

LUMBAR VERTEBRAE (Fig. 51)

The transverse and neural processes reach their greatest lengths on lumbars 1-3. In MM16, maximum length of the transverse process is 95mm, that of the neural process 90mm. In QMJM4752 the last 2 lumbars have reduced metapophyses, but they have no mammillary processes or ridges.

CAUDAL VERTEBRAE (Figs 52,53)

The transverse processes are directed anteriorly from Ca2, and by Ca3 the tips of the transverse processes reach in front of the anterior face of the centrum. The greatest widths of the transverse processes are on Ca1-5. From about Ca10, the transverse processes are sharply bent forward (Fig. 52B). The last transverse process is on Ca16-17. The last neural process is on Ca19-21; up to Ca17-18 have metapophyses. In QMJM4729 there is one transitional, globular vertebra and the last 9 caudals are dorsoventrally compressed (Fig. 53A,B); in QMJM511 there are two globular, transitional vertebrae.

CHEVRONS (Fig.54)

QM JM511 has 20 definite chevrons, with possibly a 21st. The next most complete set of chevrons is in MM1015, with 19 chevrons plus 2 small nodules. QMJM4729 and 4752 have 17 chevrons but no nodules.

The first chevron has unfused, asymmetrical arms, with a strongly developed anterior spine and 2 dorsal attachment points on the larger left arm (Fig. 54). In MM334 the chevron is enclosed in thick ligament. The anterior projection and the two dorsal projections are each linked to the posteroventral face of a vertebral centrum; i.e the chevron span three vertebrae. Subsequent chevrons have fused, equilateral arms, presenting more typical Y or V shapes in anterior view.

RIBS

QMJM511, QMJM4752 and MM333 have 13 ribs (one pair reduced in QMJM4752 and

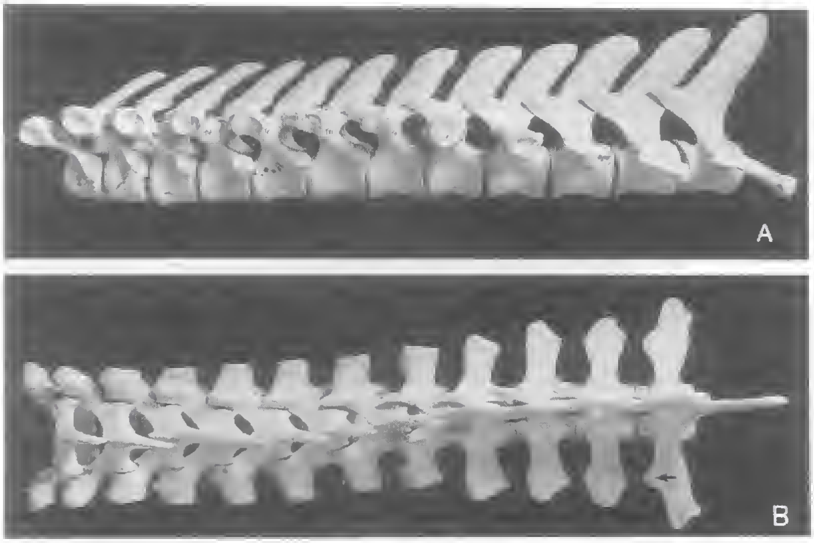

FIG. 50. Thoracic vertebrae of QMJM4729. A, Lateral view. B, Dorsal view. Note antrorse spine (arrow) on transverse process of last thoracic vertebra.

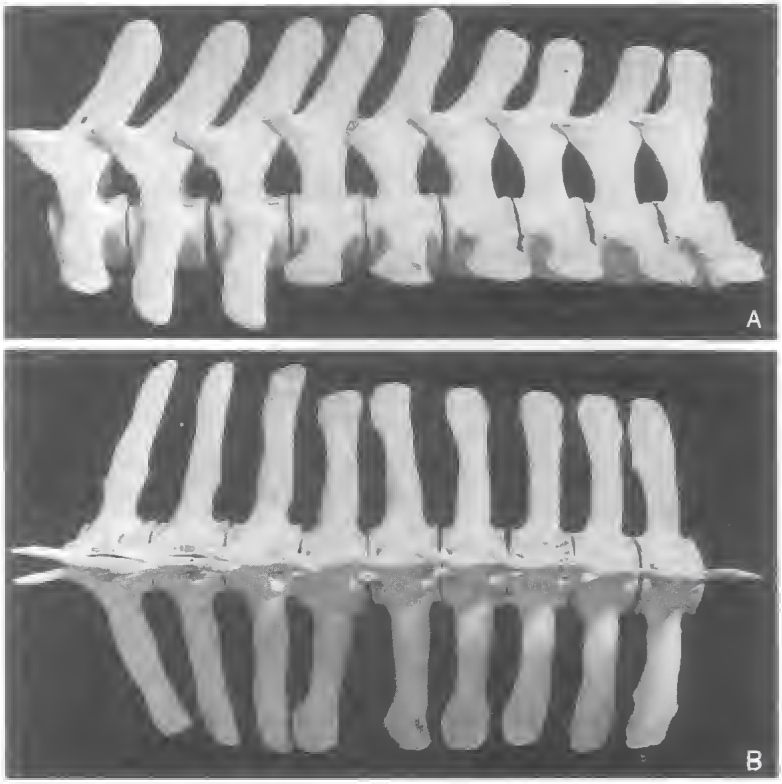

FIG. 51. Lumbar vertebrae of QMJM4729. A, Lateral view. B, Dorsal view. Note the maximum development of transverse processes on anterior lumbar vertebrae.

QMJM511) of which 8 are bicipital. MM1015 and MM92 have 12 ribs, 7 of which are bicipital.

STERNUM (Fig. 55)

The sternum is variable in shape with no apparent sexual dimorphism. A conspicuous foramen is consistently present in the manubrium between the facets for the first two pairs of sternebral ribs. The anterior facets are laterodorsal in position. In MM1015 there are 5 pairs of articular facets, but 7 pairs of sternebral ribs; the fifth and sixth sternebral ribs articulate with the last facet while the last sternebral rib pair is free.

HYOID APPARATUS (Fig.56)

The fused basi-thyrohyals form a slender arcuate transverse bar with no obvious sexual dimorphism. The stylohyals are stout, slightly curved and flattened rods.

PELVIC BONES

The small pelvic bones are variable but generally are elongate with a lateral tubercle anteriorly. Not enough material from sexed individuals is available to determine sexual dimorphism. The pelvic bone of MM333 is short and broad, but larger individuals of both sexes have more elongate pelvic bones.

SCAPULA (Fig. 57)

The scapula is distinctly longer than deep, with a distinct anterolateral ridge marking the supraspinatus fossa (terminology from Rommel, 1990), which is 22.3-27.8% of the maximum scapula length. The acromion process is consistently larger than the coracoid process, expanded distally to form a broad triangle, which can have a slightly emarginate or concave distal margin.

FLIPPER BONES

The humerus is elongate (Fig.48). There is a broad, laterally placed humeral condyle and a low medial 'common tubercle'. The delto-pectoral tuberosity on its anterior margin can extend to the distal end but is usually subdistal to the epiphyseal suture (Fig. 48).

The olecranon process is usually prominent (Fig. 48A,B). However, the ulna can become partially fused with the humerus, with no signs of an olecranon process (Fig. 48C). The 5 carpal bones are usually distinct; what appear to be the radiale and intermedium can be fused (Fig. 48).

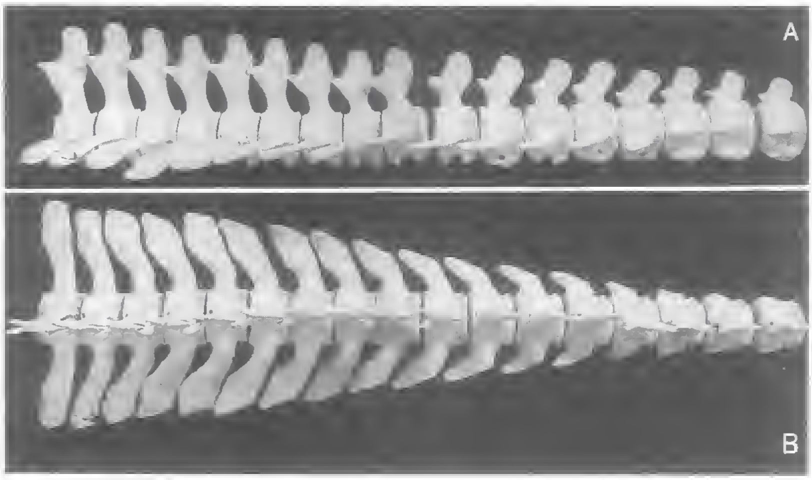

FIG. 52. Anterior caudal vertebrae of QMJM4729. A, Lateral view. B, Dorsal view. Note strong anterior projection of transverse processes.

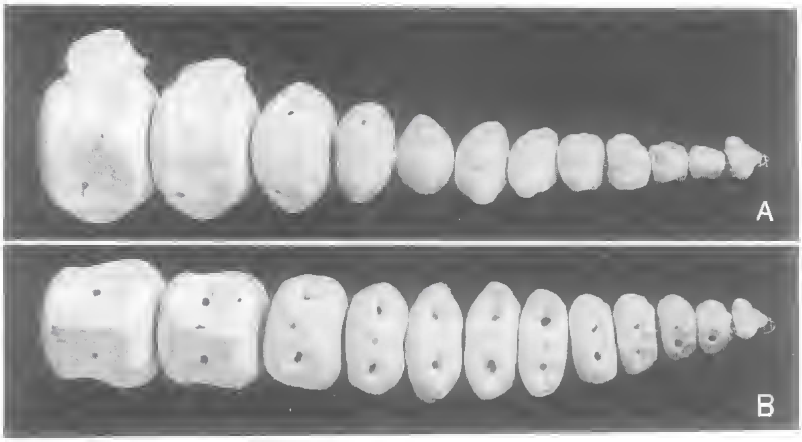

FIG. 53. Posterior caudal vertebrae of QMJM4729. A, Lateral view. B, Dorsal view.

FIG. 54. Chevrons of MM1015, lateral view.

DISCUSSION

COMPARISONS WITH SOUTHEAST ASIAN ANIMALS

VERTEBRAL COLUMN. The number of vertebrae from Qld animals is lower than in SE Asian animals (58-60 (61?) vs 62-63).

Anderson (1879:409) gave a formula for *Orcaella* of C7, T12-13, L13-14, Sa2, Ca27-28 = 62-63. For *O. 'fluminalis'* the formula was C7, T13, L16, Ca26 =63 (actually =62, Anderson, 1879:366). Given the variability in published figures (see below) and the limited number of animals examined, it is impossible to assess the significance of these differences. Differences are not, however, related simply to differences in the sizes of animals examined. Our specimens are

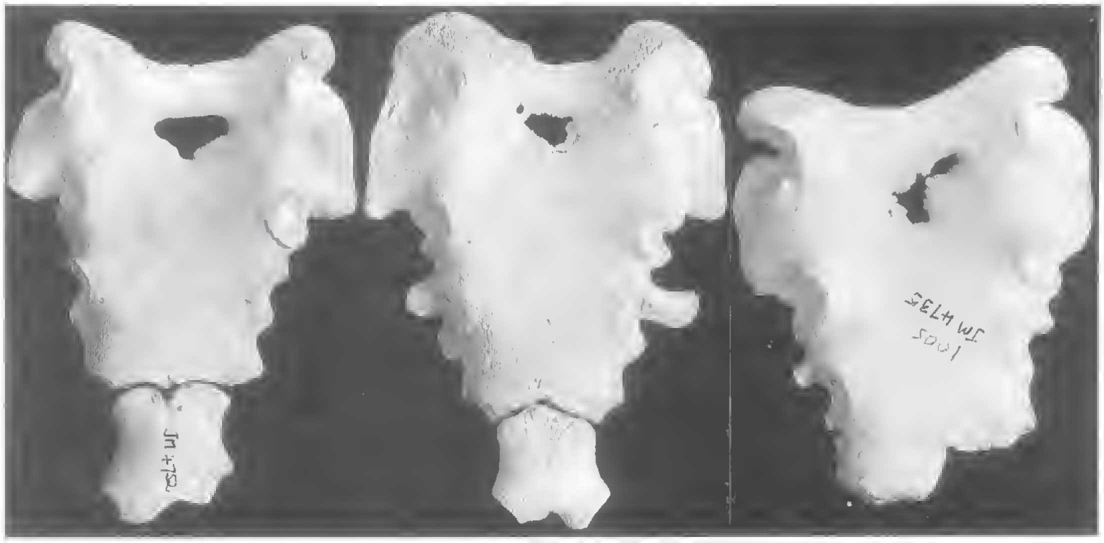

FIG. 55. Dorsal views of sternum from: A, QMJM4752; B, QMJM4729 & C, QMJM4735. Note broadly concave anterior margin, anterior foramen, dorsolateral orientation of facets for anterior sternebrae, and compound nature of sternum (A,B).

1.3-2.4 m long, which overlaps the lengths (1.8-2.3 m) of Anderson's (1879) specimens.

There is difficulty in assessing whether vertebrae are thoracic or lumbar when there are reduced ribs free from the vertebral column. In QMJM511, there are 13 pairs of ribs (last reduced) but only 12 vertebrae with articular facets. Functionally, there are 13 thoracic vertebrae, but only the first 12 would be recognized as thoracic, based on vertebral morphology. We ignored these riblets in the vertebral formula, as did Lloze (in deSmet,1977).

Anderson (1879) noted that sacral vertebrae of *O. brevirostris* have transverse processes, with contracted bases and distal expansions. We do not see this distinction in our material. Sacral vertebrae are not generally recognized in cetaceans (deSmet,1977;Rommel,1990).

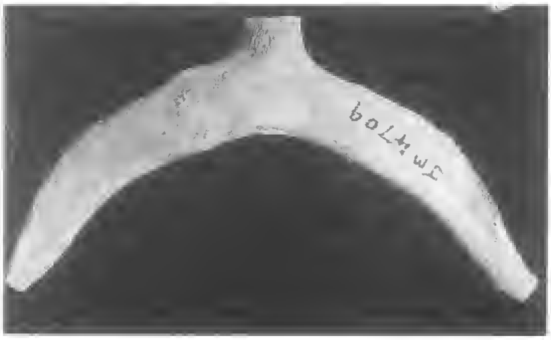

FIG. 56. Fused basi-thyrohyal bones, QMJM4709.

We follow Rommel (1990) in defining the 1st caudal as that vertebra with a chevron posterior to its centrum (cf deSmet, 1977). This is complicated in *Orcaella* by the elongate, possibly compound, form of the 1st chevron. In MM333 and MM334 which we dissected, the two dorsal projections of the left chevron are each associated with a separate vertebra. In MM334, the anterior projection is also closely associated with a third vertebra. In MM333, the underside of the first centrum is intermediate, lacking the sharp keel typical of lumbar vertebrae and the broad triangular facet for the attachment of chevrons seen on most caudals. In MM334, the vertebra linked with the anterior projection of the first chevron has a sharp keel and would have been classified as lumbar on this basis; the next two vertebrae have broad tubercular facets typical of caudal vertebrae. Only the vertebrae associated with dorsal projections of the chevron are considered as caudal vertebrae.

Anderson (1879:412) noted that in *O. brevirostris* the chevrons begin between the 34th and 35th vertebrae. Using Rommel's (1990) definition, the first caudal vertebra would be the 34th. For *O. 'fluminalis'*, Anderson (1879: 408) noted that chevrons started between the 34th and 35th vertebrae (although elsewhere he gave the position as between L12-13).

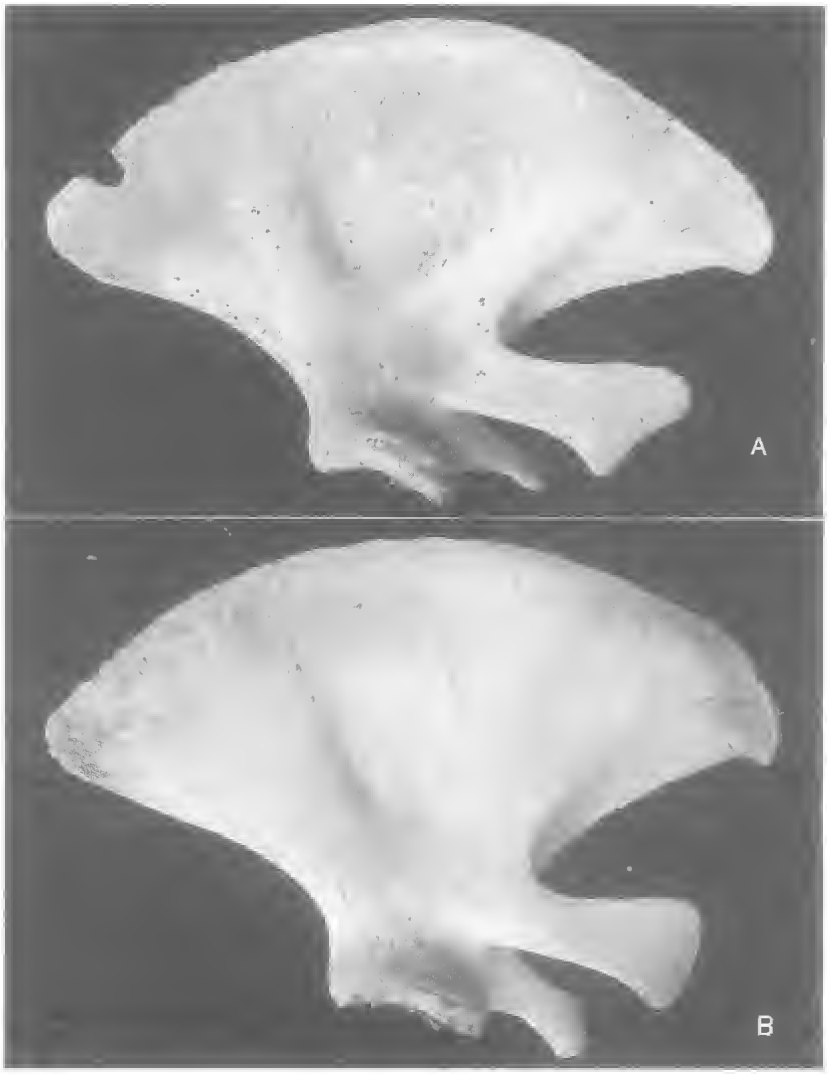

FIG. 57. Lateral view of right scapula. A, QMJM4720. B, QMJM4726. Note well developed acromion process, with triangular distal expansion.

The revised formulae for *O. brevirostris* and *O. 'fluminalis'* would thus be C7, T13, L13, Ca28-29=62-63 and C7,T13, L13, Ca29=62. The formula for an *Orcaella* from the Mekong River was C7, T12, L15, Ca28=62 (de Smet, 1977, adjusted for the difference in defining caudal vertebrae). Lloze (MS, and in Marsh et al., 1989) gave a formula of C7, T13, L16, Ca26-27=62-63.

CHEVRONS

In our material only the first chevron is unfused; Anderson (1879) noted that the first two chevrons are unfused, as are those from chevron 20 posteriorly. Anderson did not describe the shape of the first chevron but noted it articulated 'to the anterior and posterior surfaces of the 34th vertebra'. This implies that there were 2 dorsal projections, as in our material.

RIBS

Anderson (1879), in describing *O. 'fluminalis'*, noted that there were 13 'true' ribs with 'a free floating' rib 'considerably removed from the vertebral column'. In his diagnosis of the genus he noted 12-13 vertebral ribs , with 1-2 free ribs. Both statements imply a total of up to 14 ribs.

Lloze (MS; in deSmet, 1977) also noted 13 pairs of ribs, with a 14th pair free from the vertebral column. MM333 has 13 pairs of ribs, but other Australian specimens have 12 vertebral ribs, sometimes with a 13th free pair of reduced riblets. It is unlikely that the free riblets have been overlooked in those animals where only 12 pairs of ribs were collected.

STERNUM

This is variable (Fig. 55). Our specimens more closely resemble the description and illustration for *O. 'fluminalis'* in Anderson (1879, pl. 43, fig. 10), than *O. brevirostris* (pl. 43, fig. 5). Although Anderson did not illustrate a foramen in the manubrium, he noted it in *O. brevirostris*. None of the sterna illustrated by Anderson or Pilleri & Gihr (1973-1974) are compound, whereas most of Qld specimens have a smaller posterior piece as well as the manubrium (Fig. 55A,B). MM334 has a median slit running from the posterior end to the level of facets for the second pair of sternebral ribs. This is an even more extensive development of the 'deep wide notch' than noted in *O. 'fluminalis'* by Anderson (1879).

PELVIC BONES

The elongate pelvic bones of Qld animals correspond well to the illustration in Anderson (1879, pl. 42, fig. 11). The pelvic bones illustrated by Pilleri & Gihr (1973-1974, pl. 27, fig. 4) appear to be stylohyals.

SCAPULA

The scapula from Qld specimens correspond more to Anderson's (1879, pl. 43, fig. 11) illustration of *O. 'fluminalis'*, but given the variability in our small series there is no basis to separate *O. 'fluminalis'* and *O. brevirostris*. The major distinction in our material from previous descriptions is that the acromion process is generally larger than the coracoid process (Fig. 57) which is opposite to the situation in SE Asian animals (Anderson, 1879; Pilleri & Gihr, 1973-1974, pl. 26).

APPENDIX 5: NOMENCLATURE

The author citation for *O. brevirostris* is generally given as (Gray, 1866). It is generally recognized, however, that the first description of the species was by Sir Richard Owen. This inconsistency is apparent in the synonymy given by Hershkovitz (1966), where in the space of 5 lines the authority was given as '*Orcaella brevirostris* Gray' but the type species was given as '*Orcaella brevirostris* Owen, by monotypy'.

Owen gave an extensive description of the skull of *Phocaena (Orca) brevirostris*, which was read June 20, 1865. The account was not published, however, until the following year. The volume is dated 1869, but independent evidence (Zoological Record 1867) indicates that Owen's article was available in 1866; Johnson (1964) gave the publication date as August 15, 1866. In the meantime (March 1866, according to Johnson (1964)) Gray included an account of '*Orca brevirostris*' in his Catalog of the seals and whales in the British Museum. He attributed *Phocaena (Orca) brevirostris* to the unpublished account by Owen ('Zool. Trans v, ined') and included (also attributed to Owen) an extensive extract of the description and a figure by that worker.

The description and species name were attributed to Owen by Gray. Thus following Ride et al. (1985:91, article 50) and ICZN Recommendation 51B, we consider the appropriate author citation to be *O. brevirostris* (Owen in Gray, 1866).